SHOUT
SHARE
IT

7-6-68

SB.M

1020

BRITISH MU
20 AUG 19
NATURAL HIST

BULLETIN OF
THE BRITISH MUSEUM
(NATURAL HISTORY)

GEOLOGY
VOL. VII
1962-1963

TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)
LONDON: 1964

DATES OF PUBLICATION OF THE PARTS

No. 1. 15th May 1962
No. 2. 15th May 1962
No. 3. 14th August 1962
No. 4. 14th August 1962
No. 5. 14th August 1962
No. 6. 7th December 1962
No. 7. 7th December 1962
No. 8. 8th February 1963
No. 9. 9th July 1963

PRINTED IN GREAT BRITAIN
BY THOMAS DE LA RUE &
COMPANY LIMITED LONDON

BRITIS
20
NATURA

CONTENTS

GEOLOGY VOLUME VII

PAGE

No. 1. A new Eocene Primate Genus, *Cantius*, and a Revision of some allied European Lemuroids. E. L. Simons 1

No. 2. The Brachiopod Genus *Cyclothyris*. E. F. Owen 37

No. 3. The Trilobites of the Caradoc Series in the Cross Fell Inlier of Northern England. W. T. Dean 65

No. 4. Fossil Flora of the Drybrook Sandstone in the Forest of Dean, Gloucestershire. K. M. Lele & J. Walton 135

No. 5. Fossil Insects from the Lower Lias of Charmouth, Dorset. F. E. Zeuner 153

No. 6. The English Cretaceous Turritellidae and Mathildidae (Gastropoda). H. L. Abbass 173

No. 7. The Morphology of *Tubicaulis africanus* sp. nov. a fossil fern from Tanganyika. H. S. Holden & W. N. Croft 197

No. 8. The Ordovician Trilobite Faunas of South Shropshire, III. W. T. Dean 213

No. 9. The Gastropod Genus *Thatcheria* and its Relationships. A. J. Charig 255

Index to Volume VII 299

.M.A.U.

A NEW EOCENE PRIMATE GENUS, *CANTIUS*, AND A REVISION OF SOME ALLIED EUROPEAN LEMUROIDS

BRITISH MUSEUM NATURAL HISTORY
4 JUN 1962

E. L. SIMONS

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 7 No. 1
LONDON: 1962

A NEW EOCENE PRIMATE GENUS, *CANTIUS*, AND A REVISION OF SOME ALLIED EUROPEAN LEMUROIDS

4 JUN 1962

BY

ELWYN L. SIMONS

Peabody Museum and Department of Geology, Yale University, New Haven, Conn.

Pp. 1–36 ; *Pls.* 1–3 ; 4 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 7 No. 1
LONDON : 1962

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

This paper is Vol. 7, No. 1 of the Geological (Palaeontological) series.

© Trustees of the British Museum 1962

PRINTED BY ORDER OF THE TRUSTEES OF
THE BRITISH MUSEUM

Issued May, 1962 *Price Fifteen Shillings*

A NEW EOCENE PRIMATE GENUS, *CANTIUS*, AND A REVISION OF SOME ALLIED EUROPEAN LEMUROIDS

By ELWYN L. SIMONS

CONTENTS

Page
I. A NEW EUROPEAN OMOMYID *Cantius* 3
Taxonomic Revision 5
II. REVISION OF THE SPECIES OF *Protoadapis* Lemoine 8
III. NOTES ON *Pronycticebus gaudryi* GRANDIDIER 14
IV. THE TAXONOMIC POSITION OF *Anchomomys* STEHLIN 21
V. RELATIONSHIPS OF EARLY TERTIARY LEMUR-LIKE PRIMATES . 23
VI. CLASSIFICATION OF EUROPEAN EOCENE PRIMATES . . . 27
VII. CONCLUSIONS 34
VIII. ACKNOWLEDGEMENTS 34
IX. REFERENCES 34

SYNOPSIS

Cantius, a new European early Eocene lemur-like Primate genus, is described and additions to knowledge of anatomy and affinities for three Eocene lemuroid genera, *Protoadapis*, *Pronycticebus* and *Anchomomys* are made. The significance of the terms " tarsioid " and " lemuroid " is discussed as these concepts bear on a consideration of the relationships of early Cenozoic European and American lemur-like Primates to each other and to contemporary tarsier-like prosimians. The classification of European Eocene Primates is revised from Simpson (1945) and the conclusions drawn that some European Eocene lemuroids may relate closely to subsequent stocks as well as to American prosimian families contemporary with them.

ABBREVIATIONS

A.M.N.H.—American Museum of Natural History, New York.
B.M.N.H.—British Museum (Natural History).
G.P.I.H.—Geological and Paleontological Institute, University of Halle/Wittenburg.
M.C.Z.—Museum of Comparative Zoology, Harvard.
P.U.—Princeton University.
S.M.G.C.—Sedgwick Museum of Geology, Cambridge.

I. A NEW EUROPEAN OMOMYID *CANTIUS*

A RECENT examination of fossil mammals from the London Clay at the British Museum (Natural History) resulted in the discovery of an undescribed upper and two partial lower dentitions of *Protoadapis eppsi* Cooper (1932). The specimens belong to a new genus which can be assigned to the prosimian family Omomyidae.

Gazin (1958 : 47) proposed family status for the Omomyinae, which have previously been ranked as a subfamily of Anaptomorphidae. The latter taxon is now understood to be a separate stock primarily characterized by reduced dental formula and much enlarged third and fourth premolars. There are at least two European primate species, *Cantius eppsi* (described below) and *Teilhardina belgica*, which can best be assigned to the Omomyidae, although each presents some features of difference from typical omomyids. One might establish a new family or subfamily for these European species, but until they are better known such a procedure has little to recommend it.[1] Higher categories among early Cenozoic Primates have already been too much multiplied. This may be due principally to the difficulties of grouping species which are usually known only from dentitions, on rare occasions associated with fragmentary skeletal materials, and to the emotional element involved in the study of human relatives and ancestors, deservedly criticized by Simpson (1945 : 181) and elsewhere, and which, apparently, has even pervaded some discussions of fossil prosimians. Both *Cantius* and *Teilhardina* come from deposits containing Sparnacian (early Eocene) faunas and consequently represent some of the oldest Old World Primates. They are the earliest, in fact, that could possibly be near the basal stock or ancestry of any of the surviving European, Asian, or African members of the order.

Evidence as to whether or not Eocene omomyids were more lemur-like or more tarsier-like is scanty, for skull parts, other than maxillae, are practically unknown in this group. Hürzeler (1948) appears to be correct in stressing dental similarities between the early Eocene primate *Teilhardina*, from Belgium, and the much better known necrolemurines. This view is shared by the writer and is also implied by Gazin (1958 : 92). The Necrolemurinae are quite definitely tarsier-like, and close correspondence between premolar and molar cusp patterns in unspecialized necrolemurines and omomyids reinforces the idea that *Omomys* and its allies are nearer to true tarsioids than to such distinctly lemuriform Primates as *Adapis* or *Pronycticebus*. There is a reasonable probability that necrolemurines, North American omomyids, and even Old World Anthropoidea were derived from a form *like* the generalized prototarsioid *Teilhardina*, which has a lower dental formula of 2.1.4.3., and which lacks specializations in known parts that could rule out this possibility. Of course, *Teilhardina* itself, of Sparnacian Eocene provincial age, occurs too late in time to have such a position.

A skull fragment of an omomyid, *Hemiacodon*, discussed and illustrated by Gazin (1958 : 55, pl. 4, fig. 4) indicates some expansion of the dorso-frontal area in at least one member of this family—together with reasonably large orbits. Between the orbital apertures the rostrum, however, is relatively broader than in the probably omomyid derived genus *Necrolemur*, being about as in *Microchoerus* (S.M.G.C. 9669). In degree of forward rotation the orbits of *Hemiacodon* appear to be intermediate between these latter two necrolemurines.

Simpson (1940 : 190–197) discussed a pelvis, some vertebrae, and some elements of the hind limb which probably belong to *Hemiacodon* (A.M.N.H. 12613) and concluded that the " skeleton of *Hemiacodon*, as far as known, is at least as lemuroid as tarsioid, probably more ". Such judgements ultimately depend on how these two concepts are defined. It seems unlikely that the features of the postcranial skeleton in any Eocene primate would be closely similar to those in a highly specialized modern form like *Tarsius*. The earliest tarsioid *postcranial* distinctions remain elusive. Segregating out osteological characters of value in determining earlier radiations of higher categories, or in indicating phyletic relationships, is always difficult and uncertain. Nevertheless, an attempt to do so can be made for *Tarsius*. In the class of late and unusual specializations (of uncertain value in determining tarsioid phylogeny) may be the following characters : (1) Much enlarged orbits with flaring bony rims. (Occurring also, in a somewhat less exaggerated form, among other primarily nocturnal animals, such as *Nycticebus*, *Aotes*, owls, etc.) (2) Greatly elongated calcaneum and astragalus. (This specialization is seen elsewhere in galagos and in an analogous way in anurans.) (3) Fused tibia and fibula. (Such fusion occurs in a variety of hopping tetrapods including many rodents, lagomorphs, in some marsupials and insectivorans, as well as among Aves. See Barnett & Napier (1953 : 12) for further discussion of the adaptive significance of this feature.) Should these characters be relatively recent acquisitions among tarsiines, even the direct Eocene ancestor of *Tarsius*, in lacking them, would be difficult to distinguish from lemuroids postcranially. In view of this possibility, evidence provided by the postcranial bones of *Hemiacodon* appears to be equivocal in relating the animal either to Tarsiiformes or Lemuriformes. What would help to indicate the affinities of such omomyids would be knowledge of such features as the size and shape of component parts of the brain (their size relative to each other), extent of facial shortening, proportions of palate and skull vault, amount of forward shifting of the foramen magnum, and various other characters of the basicranium, particularly degree of inflation of the auditory bullae and mastoid region, and situation or relationships of entocarotid circulation, of the ectotympanic pterygoid alae, and of cranial foramina. Although for omomyids these cranial features are not known they can be observed in *Necrolemur*, which in most of these areas closely resembles *Tarsius*, and which dentally (at least) shows affinity with Omomyidae.

---

[1] It also seems possible that *Periconodon*, *Lushius* and *Hoanghonius* represent three other Old World omomyids. Together with broad similarities in known parts, both of these Primates possess an unusual cusp on the antero-internal base of the protocone which has been called a pericone. This structure often occurs in *Omomys* but is known in very few other members of the order. For discussion of *Luchius*, see Chow (1961).

As knowledge of the earliest Primates grows with new finds, taxonomic separation, at all grades of classification, can be expected to become more arbitrary. In this respect, some European Primates, particularly *Cantius*, evidence a closer relationship between Notharctidae and Omomyidae than has previously been documented ; although this possibility was briefly considered by Gazin (1958 : 47). Perhaps both of these families, assuming the two groups deserve separate family status, are not far removed from a common late Paleocene ancestry.

TAXONOMIC REVISION

Genus ***CANTIUS***[1] nov.

(Pl. 1)

TYPE SPECIES. *Protoadapis eppsi* Cooper, 1932.

GENERIC CHARACTERS. As for the species.

---

[1] From the Latin for County Kent, England (*Cantium*, *Cantia*) in which all specimens of this primate have been discovered and in analogy with such related forms as *Washakius*, from the North American Eocene.

DISCUSSION. Size : *Cantius* is a large omomyid, intermediate in size between *Hemiacodon* and *Ourayia*, but distinctly smaller than any of the species of *Protoadapis*, and may have been about the size of the living African Giant Galago, *Galago crassicaudatus*.

The discovery of a right maxilla with P^3–M^3 of this species (Pl. 1*a*) from the early Eocene deposits at Abbey Wood, Kent (since Cooper's original description) confirms that the species belongs to a genus distinct from *Protoadapis*, a conclusion which can also be demonstrated by features of the lower dentition of *Cantius eppsi* (B.M.N.H., M–13773) originally reported on by Cooper (1932), and by two other partial lower dentitions found subsequently (Pl. 1*b*). Indeed, Cooper himself suggested the possibility that the British species belonged to a distinct genus. Re-examination of all available specimens of *Protoadapis* indicates that this is so.

Some differences between *Cantius* and *Protoadapis* (in the lower dentition) are that the former is somewhat smaller, has paraconids on P_4, M_1, M_2, a much longer and more complex M_3 talonid, and a considerably smaller and lower P_3. A characteristic feature of *Protoadapis*, sometimes seen in species of the North American genus *Pelycodus* as well, is that the P_3 stands noticibly higher than P_4. In *Protoadapis* the paraconid decreases in expression posteriorly in the molar series but not in the same way as in *Cantius* where the paraconid and metaconid are increasingly drawn together in the series M_{1-3}, compare Pls. 1*b* and 3*f*. Throughout the lower molar series of *Protoadapis* the paraconid remains widely separated from the metaconid and in M_3 is represented only by a slight crest—still considerably removed from the metaconid. In *Cantius* paraconids are clearly delimited in all three molars and are nearly as high as metaconids.[1]

In this progressive alteration of trigonid elements posteriorly *Protoadapis* resembles closely *Notharctus*, while *Cantius* is much more like some specimens of *Omomys* in which, although a distinct paraconid is retained throughout the lower molars, the paraconid is closer to the metaconid in M_{2-3} than in M_2. *Cantius*, in its enlarged and complex M_3 talonid, also agrees well with the elaboration of this element in omomyids. Yet another distinction in the lower dentition between *Cantius* and *Protoadapis* is that in *Cantius* a clearly defined paraconid cusp is present in the P_4, a structure which never occurs in *Protoadapis* (see Pl. 3*f*, and Stehlin, 1912 : 1282).

Recognition of the Abbey Wood species as generically distinct from *Protoadapis* was delayed, in part, because of the scarcity of comparative material in European museums. The total number of good specimens belonging to all species of both of these genera is probably less than ten. Nevertheless, the significance of the facts that *Cantius*, an omomyid, and *Protoadapis*, a notharctid-like adapid, occur in the European Eocene should be stressed. Knowledge of such ranges gives added import to the more extensively known North American Primates of the omomyid-notharctid type because it indicates that forms closely affined to them were present in the early Tertiary of the Old World. The possiblity is thus strengthened that some North

---

[1] Paraconid and metaconid of the M_3 in the holotype of *C. eppsi* cannot be distinguished, either because of wear or because they are coalesced. In B.M.N.H., M–15147*a*, *b*, however, these M_3 cusps are separate but closely approximated.

American species may approximate morphological, or even linear stages in the ancestry of Old World Primates.

The upper dentition from the Abbey Wood locality (Pl. 1*a* ; B.M.N.H., M–15145)—quite apart from its occluding well with the type lower dentition of *Cantius eppsi* (both are of the right side)—shows definite omomyid affinities to about the same degree as do the lower teeth. Hence there is little reason to doubt that it can be assigned to *Cantius eppsi*. Taken as a whole, this upper dentition is close to that of *Omomys* and of *Teilhardina* but is one-half larger than that of either of these small Primates. P^3 and P^4 are rather simple teeth with a constriction between the inner and outer cusps and are similar in conformation to those of *Omomys*, *Teilhardina* and *Hemiacodon*. P^3 has but a single outer and inner cusp and is smaller relative to P^4 than in some specimens of *Omomys*. Both P^3 and P^4 are less crenulate than in *Hemiacodon*, but exhibit slight enamel wrinkling, particularly on the median slope of P^4 protocone. P^4 carries a small cuspule on the anterior slope of the outer cusp which occurs also in *Hemiacodon* and *Washakius*, but apparently not in typical *Omomys*. The anterior, median and posterior protocone crests of the P^4 of *Cantius* are situated about as in *Washakius* (see Gazin 1958, pl. 9, No. 1).

An interesting similarity of *Cantius* to necrolemurines (and to *Tetonius* as well) is that the posterior protocone crest of M^1 and M^2 turns down toward the posterolingual part of the basal protocone cingulum, thus breaking the ridge running toward the metaconule. This forms a so-called " nannopithex-fold ". There is, however, practically no indication of an incipient hypocone element, other than a slight thickening of the posterolingual part of the basal protocone cingulum. As in other omomyids the para- and metaconules are distinct on all three upper molars. These elements are usually less well defined in notharctids. Also unlike notharctids *Cantius* lacks any suggestion of an upper molar mesostyle. Molar para- and metacones are connected by straight crests on their facing slopes, much as in *Omomys* and *Washakius*. Nearly continuous lingual and labial basal molar cingula in *Cantius* are also quite like those of *Omomys*. Another resemblance to *Omomys*, to *Teilhardina*, to some of the more generalized late Paleocene Primates particularly *Navajovius*, and also to *Tetonius* is the small size of the M^3 compared to M^{1-2}. Para- and metastyle elements are present, as in most omomyids, except on M^3 metacone.

The recent identification of an upper dentition of *Protoadapis* in the collections of the Geological Institute of the University of Halle/Wittenburg makes possible further comparative remarks about it and *Cantius*. *Protoadapis*, unlike *Cantius*, shows no indication in the upper molars of a nannopithex-fold, and the internal cingulum is typically pronounced and continuous around the lingual base of the protocone, the hypocone is large, and there is no indication of a metaconule on any of the upper molars, see Pl. 3. In these differences from *Cantius*, *Protoadapis* more closely resembles the notharctid *Pelycodus*.

In conclusion, *Cantius* has not been found to exhibit any features of resemblance to notharctids or adapids not occurring in the North American Omomyidae, and in view of numerous similarities to *Omomys* and *Hemiacodon* it is assigned to the latter family. The dental formula of *Cantius* is apparently more reduced than in *Teilhardina*, but evidence regarding the exact number of antemolar teeth remains inadequate.

Cantius eppsi (Cooper)

(Pl. 1)

1932. *Protoadapis eppsi* Cooper, p. 461, pl. 11, figs. 2, 3.

HOLOTYPE. Right ramus of mandible with P_3–M_3 and partial alveolar borders of I_3–P_2, B.M.N.H., M–13773.

MATERIAL. B.M.N.H., M–13773 (Holotype), B.M.N.H., M–15145, maxilla with P^3–M^3; B.M.N.H., M–15147*a*, mandibular fragment with M_1–M_3; and B.M.N.H., M–15147*b*, mandibular fragment with M_{2-3}.

HORIZON AND LOCALITY. Blackheath Beds (Sparnacian); Abbey Wood, one and three-quarter miles east of Woolwich, Kent.[1]

DESCRIPTION. *Lower dentition:* Dental formula: 2(?).1.3(?).3. One small incisor alveolus, followed by a much larger canine alveolus, narrow anteroposteriorly and broad buccolingually. If only one premolar was present anterior to P_3 it may have been two-rooted. Two-rooted P_3 with crown lower than P_4 and lacking distinct para- and metaconids. Para- and metaconids well developed on P_4, connected to protoconid by crests; well-defined central crest on talonid, running posteriorly along mid-line of tooth from protoconid and with small posterior cuspule; P_4 not molarized. Trigonid of M_1 large, with three well-separated cusps; paraconid and metaconid joined to protoconid by low ridges; talonid much larger than trigonid with distinct ento- and hypoconid, small hypoconulid present on slope of posterior crest of hypoconid. Outline of M_2 (crown view) more nearly circular than that of M_1, as in *Ourayia*, *Hoanghonius*, etc. M_2 trigonid broad transversely, narrower anteroposteriorly, with more closely approximated paraconid and metaconid than M_1. Paraconid and metaconid of M_3 trigonid either coalesced as a single cusp (M–13773) or closely approximated (M–15147*a* and *b*).

Upper dentition: B.M.N.H., M–15145: P^{3-4} with slight constriction between protocone and outer cusp. P^4 with small anterior cuspule, as in *Hemiacodon*. M^2, M^1, M^3; no mesostyle or distinct hypocone on upper molars; antero-internal base of molar protocone projecting most mesiad; nannopithex-fold present on posterior slope of M^1 and M^2; paraconule and metaconule present on M^{1-3}.

II. REVISION OF THE SPECIES OF *PROTOADAPIS* LEMOINE

History of Study

Preparation of the foregoing section on the British early Eocene primate *Cantius* necessitated investigation of all the available material of *Protoadapis*. It soon became clear that species of this genus were much in need of revision.

Unfortunately Stehlin's discussion of members of *Protoadapis* (1912: 1284–1286) intruded some taxonomic confusion, as well as a misspelling of the generic name; this was largely corrected by Teilhard (1921: 66, 67, 88–91) but Stehlin's views, and additional misconceptions of dating quoted by Osborn (1890: 55) have continued to

---

[1] Dr. G. G. Simpson of Harvard University has suggested in a personal communication that the species of *Hyracotherium* from Abbey Wood indicate an earliest Eocene age for this fauna. This is also indicated by an M_3 of *Coryphodon* from the same locality figured by Cooper (1932: 459).

Measurements (in mm.) of Cantius eppsi *(Cooper)*

(All specimens in the British Museum of Natural History)

Mandible:		M–13773	M–15147a	M–15147b
Depth of jaw beneath M_2		6·7	—	—
Anteroposterior length of P_3–M_3		17·2	—	—
Anteroposterior length of M_{1-3}		11·4	11·5	—
Anteroposterior length of M^{2-3}		8·1	8·0	8·2
Anteroposterior diameter of	P_3	2·8	—	—
	P_4	3·3	—	—
	M_1	3·6	3·6	—
	M_2	3·6	3·7	3·8
	M_3	4·5	4·3	4·4
Transverse diameter				
(trigonid)	P_3	1·8	—	—
	P_4	2·3	—	—
	M_1	2·5	2·3	—
	M_2	3·3	3·0	3·1
	M_3	3·0	2·9	3·1
(talonid)	M_1	2·8	2·8	—
	M_2	3·1	3·0	3·2
	M_3	2·4	2·4	2·8

Maxilla: M–15145			
Anteroposterior diameter of P^3		15·0	(Transverse diameter)
Anteroposterior diameter of	P^3	3·0	3·2
	P^4	3·0	3·8
	M^1	3·6	4·7
	M^2	3·7	5·4
	M^3	3·0	4·3

affect the literature on this primate. These errors were largely reproduced by Hill (1953 : 482–487).

Further complications derive from the observation, made during a recent visit to the Halle/Wittenburg Geological and Paleontological Institute, that the holotypes of two Eocene Primates, " *Europolemur* " *klatti* and " *Megatarsius abeli* " described by Weigelt (1933) can be assigned with confidence to *Protoadapis.* As it was not possible for Weigelt (1933) to make direct comparisons with previously described fossil Primates some specific and generic assignments which might have been recognized for the Geiseltal species were not noted by him. In fact, at that time Weigelt probably could not have determined his two new genera as upper dentitions and skulls of *Protoadapis,* since the associated upper and lower dentition, G.P.I.H. 4310, discussed below, had not then been discovered.

The assumption that species of this genus occur in the French Paleocene of Cernay and Rilly dates from an erroneous citation in Lemoine & Aumonier (1880 : 611) as stated by Teilhard (1921).[1] However, this misapprehension was repeated in Hill

---

[1] Lemoine & Aumonier list a species of this genus, *P. copei,* as occurring in the Cernay Paleocene. It was not figured or described and is now lost, probably because Lemoine later referred the specimen to a different genus and species, not *Protoadapis.*

(1953 : 483). Lemoine later stated (1891 : 28) that this genus is restricted to the Eocene. D. E. Russell who is currently revising the French Paleocene faunas, informs me that it does not occur at Cernay. The recognition of several specimens of *Protoadapis* from the Middle Eocene Brown Coals of the Geiseltal, Germany, now in the collections at Halle, serves to date the earlier members of this genus better than the rather scanty and poorly associated Cuisian fauna with which the French specimens of *Protoadapis curvicuspidens* and " *Protoadapis recticuspidens* " were recovered.

A further error in the literature on this genus is its recorded occurrence in the Belgian Eocene deposits (Hill, 1953 : 483). There is no real evidence for such a record, but a specimen of *Protoadapis* from the Quercy phosphorites of south-central France was, at the time of Teilhard's writing, in a private collection at Louvain and his reference to it may have led to this confusion of range.

All the materials of this genus discussed by Lemoine, Stehlin, and Teilhard, as well as the specimens at Halle, belong (after the removal of " *Protoadapis* " *eppsi*) to no more than three species. *Protoadapis recticuspidens* Lemoine, 1878, is based (in spite of published remarks to the contrary) on a single specimen in which the teeth are so worn that only a few characters of M_3 can be determined. This tooth, and the mandible, now in the Paris Museum, are distinctly smaller than are those of *Protoadapis curvicuspidens* (here designated as the type species of the genus) and it may not belong to *Protoadapis*. I would prefer to regard *Protoadapis recticuspidens* as a *nomen vanum*.

As Teilhard stressed, the specimen called *Protiadapis recticuspidens* by Stehlin (1912, fig. 278) is actually *P. curvicuspidens*, the holotype of which is now in the Muséum National d'Histoire Naturelle in Paris. It is on the basis of this specimen that the genus *Protoadapis* was first defined.

TAXONOMIC REVISION

Genus ***PROTOADAPIS*** Lemoine

(Text-fig. 1)

TYPE SPECIES. *Protoadapis curvicuspidens* Lemoine (1878). (Unnumbered holotype and two other specimens in National Museum of Natural History, Paris.)

AMENDED DIAGNOSIS. Size : somewhat larger than *Adapis parisiensis* ; lower dental formula : 1?.1.3.3. incisors missing in type but one or more alveoli appear to be present in other specimens ; canine large (alveolus) ; P_1 absent, replaced by diastema ; P_2 short with single pointed cusp, and with two obliquely situated roots, the anterior located more buccally. P_3 distinctly larger, much higher and more pointed than P_2 with nearly vertical anterior margin, no distinct paraconid or metaconid ; P_4 lower than P_3 (unlike *Cantius*) lacking paraconid, but with well-defined metaconid and talonid possessing central ridge ; molar paraconids reduced, but extending much more lingually than in *Adapis*, less so than in *Cantius*. M_1 and M_2 with small hypoconulid on posterior hypoconid crest ; M_3 hypoconulid making up a distinct lobe ; length from P_4 to M_3—22 mm., depth of horizontal ramus beneath M_2 from 10 to 12 mm.

Discussion. Two French species of this genus are accepted here as valid, *Protoadapis curvicuspidens* collected in Paris Basin deposits, perhaps of Cuisian age, and *Protoadapis angustidens* (Filhol, 1888) from the Quercy phosphorites (see Text-fig. 1). *Protoadapis brachyrhynchus* Stehlin (1912) is clearly a synonym of the latter species, as Teilhard (1921 : 97) concluded. A third species, *Protoadapis raabi*, from the Middle Eocene Brown Coals of the Geiseltal, Germany, is slightly smaller than

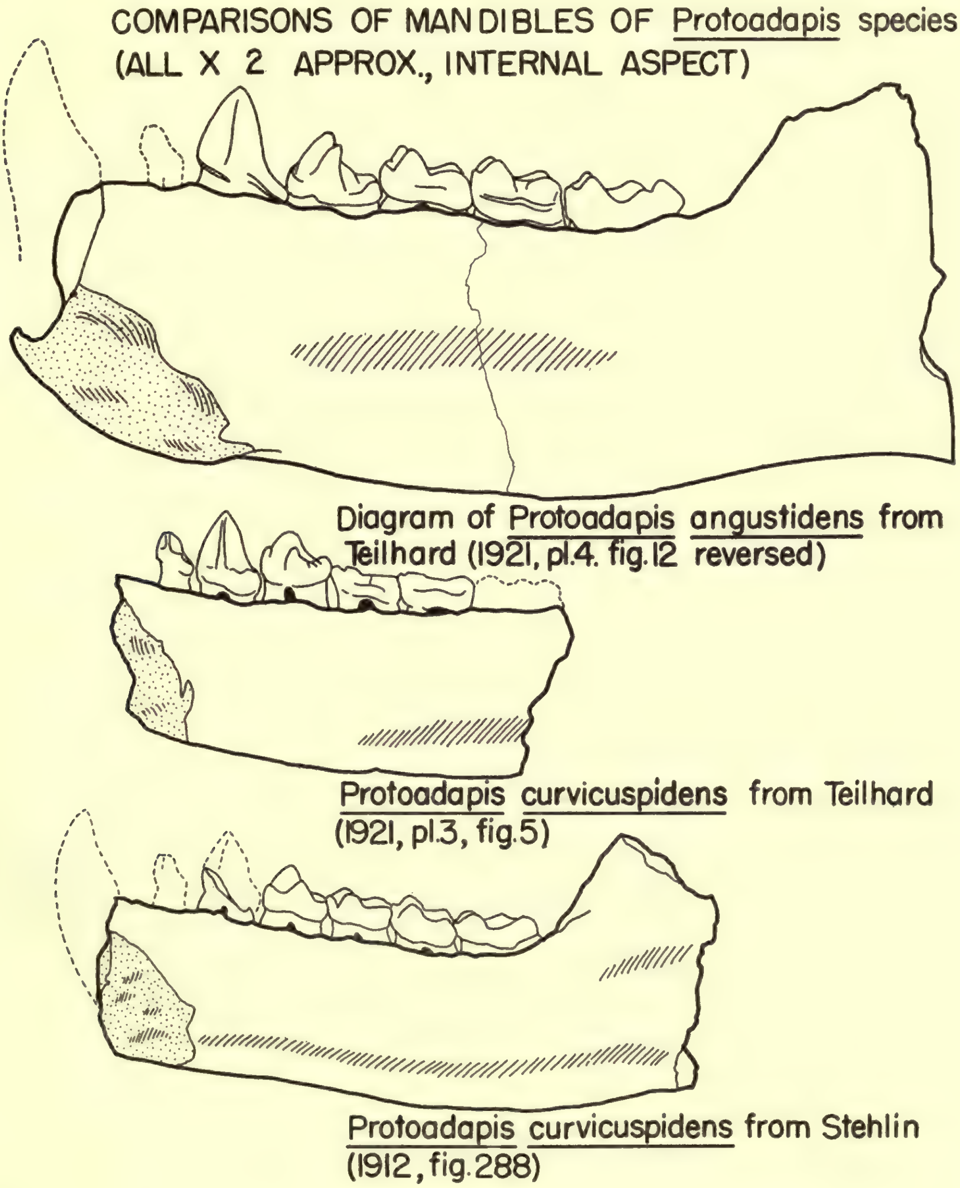

COMPARISONS OF MANDIBLES OF Protoadapis species
(ALL X 2 APPROX., INTERNAL ASPECT)
Diagram of Protoadapis angustidens from Teilhard (1921, pl.4. fig.12 reversed)
Protoadapis curvicuspidens from Teilhard (1921, pl.3, fig.5)
Protoadapis curvicuspidens from Stehlin (1912, fig.288)

Fig. 1. Species of *Protoadapis* Lemoine from French deposits.

P. curvicuspidens but does not differ greatly from it otherwise, in so far as these two species can be compared. Better materials may prove that the latter two " species " intergrade but pending such an eventuality, it is advisable to retain a separate species for the Geiseltal finds.

SPECIFIC DIAGNOSES. Teilhard (1921) has published full descriptions of the two species of this genus from the French Eocene and consequently they will not be separately diagnosed here.[1]

Protoadapis klatti (Weigelt)

(Pls. 2, 3)

1933. *Europolemur klatti* Weigelt, p. 123, pl. 4, fig. 5 ; pl. 6, fig. 4.
1933. *Megatarsius abeli* Weigelt, p. 141, pl. 4, fig. 4 ; pl. 6, figs. 1–3.

MATERIAL. In addition to the holotypes of " *Europolemur* " *klatti* and " *Megatarsius abeli* " (No. 4234) ; numbers 4238, 4258, 4280, 4292 and 4310 of the collections of the Geological and Paleontological Institute of the University of Halle/Wittenburg are referable to this species. Some of these specimens were regarded by Heller (1930) as belonging to *Adapis*, but this genus does not occur in the Geiseltal fauna.

DIAGNOSIS. A medium-sized primate—apparently about the size of *Pronycticebus* or the Recent Potto, *Perodicticus*. Dental formula : $\frac{2.1.3.3}{?1.1.3.3}$; anterior lower incisor not known (if present), I_3 procumbent and spatulate ; $\overline{C}$ long and pointed with slightly developed posterior shelf—appearance about as in *Notharctus*, $\overline{C}$ followed by diastema ; P_2 two-rooted with simple pointed crown and posterior heel, lacking metaconid and protoconid ; P_3 much higher than P_2 and P_4 and lacking protoconid ; P_4–M_3 as in *Protoadapis curvicuspidens* but smaller, M_1 and M_2 with distinct hypoconulid on posterior slope of hypocone, M_3 hypoconulid and entoconid large.

I^2 larger than I^3, spatulate with crown anteromedially directed and somewhat procumbent ; I^3 small and simple, may be separated from $\underline{C}$ by a diastema ; $\underline{C}$ much larger and longer than in *Adapis*, furrowed along its external face by anterior and posterior vertical grooves and followed by a diastema ; P^2 less than half as large as P^3, and with small protocone (two rooted) ; P^3 and P^4 with single ectoloph and large protocone ; M^1 lacking mesostyle and metaconule, but with distinct paraconule and prominent internal and external cingula, internal cingulum with large hypocone, basal cingulum sometimes incomplete across internal face of protocone ; M^2 slightly larger than M^1 with more continuous lingual cingulum and larger hypocone ; M^3 smaller than M^1–M^2, lacking a distinct hypocone, but with pronounced internal cingulum.

DISCUSSION. " Two " undescribed specimens in the Halle collection form a valuable basis for the clarification of the dental structure of *Protoadapis*. One of these G.P.I.H. 4310, from the Leonhardt Coal Mine (the locality of " *Europolemur* ") includes the left P_4 through M_3, the right M_3 an associated right lower canine and M^{1-3} (M^{1-2} somewhat damaged) see Pl. 3*e*, *f*. The second specimen, G.P.I.H. 4258 (Pl. 2), crushed facial region with attached lower jaw fragment of the left side with I^2 through P^3

---

[1] *Protoadapis angustidens* is larger and occurs later in time than *P. curvicuspidens*.

and I_3 through P_3 was also collected from Leonhardt Mine. The specimen card of No. 4310 states that these teeth probably belong to the same individual as No. 4258, and this association is reinforced by similarity of colour, wear, matrix, and the fact that the two specimens do not share any overlapping parts, which would rule out such a possibility. In any event, both are referable to *Protoadapis* and together they preserve almost the entire dentition intact. Dental comparisons indicate that the skull of " *Europolemur* " *klatti* belongs to the same species as the foregoing specimens and is therefore a synonym of *Protoadapis*. The holotype of " *E.*" *klatti* (apparently lost during the last war) has upper molars of the same size and conformation as those of G.P.I.H. 4310 (judging from Weigelt's published information) and in so far as these two finds can be compared, there is no basis for a specific distinction. Teilhard (1921, pl. 3, fig. 6) illustrated an upper left molar which he suggested might be of *P. curvicuspidens* ; this is confirmed by the Halle specimens. Because of crushing, measurements on Brown Coal fossil Primates, other than on teeth, are not very reliable and thus have reduced value when drawing taxonomic distinctions. However, the length of P^4–M^3 series of *Protoadapis klatti* is about 15 mm. in the type and the length of P_4–M_3 in G.P.I.H. 4310 is about 17·2 mm. Similar measurements for *Cantius eppsi* are 14·2 and 15·1 mm. respectively.

Regarding the teeth of " *Megatarsius abeli* " from the Cecilia Coal Mine (locality Leichenfeld II), as Weigelt noted (1933 : 142) :

> " die Beschaffenheit der Kronen ist
> eigenartig stumpf, als wenn die oberste
> Schimelzchicht fehlte . . . ".

There is no doubt that this condition is due to post-mortem chemical absorption of the enamel and some of the dentine of the canine and P^4 through M^3 of the right side (all of the dentition that remains in " *Megatarsius* "). This sort of erosion of fossil teeth is quite common in early Cenozoic mammals. Neither Heller (1930)[1] nor Weigelt (1933) appear to have taken into account the fact that many of the Geiseltal Primates have lost almost all significant dental characters in this way. Such erosion also explains the extraordinary appearance of the canine of " *Megatarsius* " figured by Weigelt (1933, pl. 6, fig. 1). In this tooth, the enamel and much of the dentine of the crown has been removed and there has also been erosion around the base of the tooth. The odd basal cingulum and the whole appearance of the tooth is unreal misleading. In " *Megatarsius* ", G.P.I.H. 4234, the upper dental formula is the same as in G.P.I.H. 4258–5310, *Protoadapis*. Furthermore, the eroded crowns of M^1 and M^2 show metaconule and mesostyle absent, but paraconule present, and allowing for the reduction in size caused by enamel erosion, M^{1-3} of " *Megatarsius* " are of appropriate size for *Protoadapis klatti*. For the writer, no doubt remains that " *Megatarsius* " is referable to *P. klatti*. In any case, G.P.I.H. 4234 is not adequate as a type specimen, and if not *Protoadapis* would be a *nomen vanum*.

Weigelt's discussion of the skulls of " *Europolemur* " and " *Megatarsius* " describes adequately these much damaged specimens. In overall morphology the skull of *Protoadapis* is more like that of *Pronycticebus* than of *Adapis*. With *Pronycticebus*, it shares a comparatively shorter rostrum, larger orbits, more slender zygoma, P^4 with a single outer cusp and two-rooted P^2, but differs in having lost P 1/1. " *Megatarsius* " has a broad interorbital septum about 1 cm. wide and resembles that of *Pronycticebus* in the disposition of the medial end of the supraorbital margin. On the antero-dorsal face of this skull between the temporal crests is a broad and slightly depressed area. The temporal ridges converge to the mid-line about 2·25 cm. behind the posterior end of the nasals. Conformation and extent of the nasals can be determined in G.P.I.H. 4234. These bones are slightly expanded posteriorly as in *Pronycticebus*. The orbital region is much crushed and, consequently, the lacrymal foramen cannot be located, but fragments suggest that the post-orbital bar was more slender than in *Adapis*.

---

[1] Heller's holotype of *Adapis minimus* is an indeterminate specimen for the same reason, all of the enamel having been removed by chemical solution.

Relationships of Protoadapis

Now that both the upper and lower dentitions and something of the skull are known in *Protoadapis*, it takes a more significant position in early Primate history. Placement of this genus as a typical lemuroid primate seems beyond doubt, and in fact it is the only Old World early Cenozoic form which has the same dental formula as any of the living lemuroids, although it lacks the specialized tooth comb below which is typical of the latter taxon. Being older, and yet having a more reduced dental formula, it cannot be near the lines which gave rise to such Eocene lemuroids as *Adapis*, *Pronycticebus* and *Notharctus*. Perhaps its greatest similarities are with *Pelycodus* and *Pronycticebus* which, however, retain P 1/1. In *Pelycodus* the manner of hypocone formation may also be different. Some specimens of *Pelycodus*, for instance A.M.N.H. 15022 (see Gregory, 1920, pl. 35), appear to have an incipient hypocone on the basal cingulum and at the same time another " pseudohypocone " developing from the nannopithex-fold on the posterior slope of the protocone. In the line leading to *Notharctus* the hypocone derived from the basal cingulum is suppressed, while in *Protoadapis* the nannopithex-fold is absent. The nearest known upper molar morphology that could give rise to both these patterns is that of *Cantius* but this form is too late to be ancestral to *Pelycodus* and its dentition too generalized for classification with the adapids. As suggested by Teilhard (1921), Simpson (1940), and others, *Protoadapis* shares with the North American notharctids many of the features which distinguish the latter group from the Adapidae. The upper dentitions and the anterior teeth preserved at Halle add somewhat to this conclusion, but in several respects this primate tends to link adapids and notharctids as *Cantius* links the omomyids with the latter families. In view of dental similarities with *Caenopithecus* and *Pronycticebus*, together with its European provenance, *Protoadapis* is here referred to the Adapidae.

III. NOTES ON *PRONYCTICEBUS GAUDRYI* GRANDIDIER

(Text-fig. 2)

The unique skull and mandibular fragment of *Pronycticebus* was discovered in 1893 and reported, in the original studies of Grandidier (1904, 1905), to be of Bartonian, late Eocene age, from Memerlein-le-Quercy in south-central France. The Abbé René Lavocat has suggested in a personal communication to the writer that judging from his studies of mammals of Oligocene provenance, there is a similarity in the colour of bone and matrix of this specimen to those of the European Oligocene. This interesting observation implies, at least, that *Pronycticebus* may be from the latest levels of the Quercy caves. If so, it could be of Stampian Oligocene provincial age.

Pronycticebus has long been a difficult form to assess taxonomically, due in part to the lack of specialization of the teeth and the presumed absence of a post-orbital bar. Grandidier originally suggested affinities with the living lorisiform Primate *Nycticebus*, hence its generic name. This view has some merit. Subsequently Gregory (1920) and others held that the species has tarsioid affinities. This conclusion appears to have been based largely on the brachycephaly of the skull (considerably more pronounced that in *Adapis* or *Notharctus*) and which, at the time of Gregory's writing, was rivalled in degree, among Eocene Primates, only by *Necrolemur* skulls (also from Quercy) and by a fragmentary skull, lacking dentition, from the Middle Eocene of North America described by Granger & Gregory (1917) as " *Aphanolemur gibbosus* ".

Gazin, in a revision of the Middle and Upper Eocene Primates of North America (1958), has shown that *Aphanolemur* is a synonym of *Smilodectes*. Several specimens figured by him indicate that expansion of the brain case in the latter primate (apparently closely related to *Notharctus*) has reached about the same level as in *Pronycticebus*. Skulls of *Smilodectes*, and to a lesser extent of *Notharctus*, demonstrate, therefore, that the degree of brain expansion which occurred in *Pronycticebus* was not unique among Eocene lemuroids. *Protoadapis*, judging from the crushed skulls at Halle, also had a rather large brain.

On other grounds, Le Gros Clark's careful study (1934) of the cranial anatomy of *Pronycticebus* has already demonstrated that this genus is not a tarsioid, a position recently re-affirmed by Piveteau (1957 : 55, 56).

Re-examination of the Evidence

Orbital Region

It is, perhaps, an amusing commentary on the nature of appraisal of fossil specimens that the zygomatic arch of the one known skull of *Pronycticebus* can be said to have been " evolving " almost continuously since Grandidier's original studies on this primate in 1904 and 1905. Apparently some time before the original description, the zygomatic arch was buried in a thick layer of plaster of Paris, which closely resembles the colour of the original bone. In 1934 Le Gros Clark remarked that the zygoma was not quite as broad as is indicated in Grandidier's illustrations and figured a narrower arch. Piveteau's plate (1957 : 61) shows a still more slender arch. In the same year, the writer was able to remove most of the remaining plaster which exposed a yet more gracile arch and the very distinct base of a post-orbital process (Text-fig. 2). Furthermore, the region of the frontal attachment of the post-orbital bar shows distinct fractures on both sides of the skull, where the bar has been broken off. The cross-sectional extent of this area is shown by hatching in Text-fig. 2. One can clearly distinguish the broken surface, and although this area of attachment is not very extensive in the vertical dimension, this correlates well the slender zygoma,

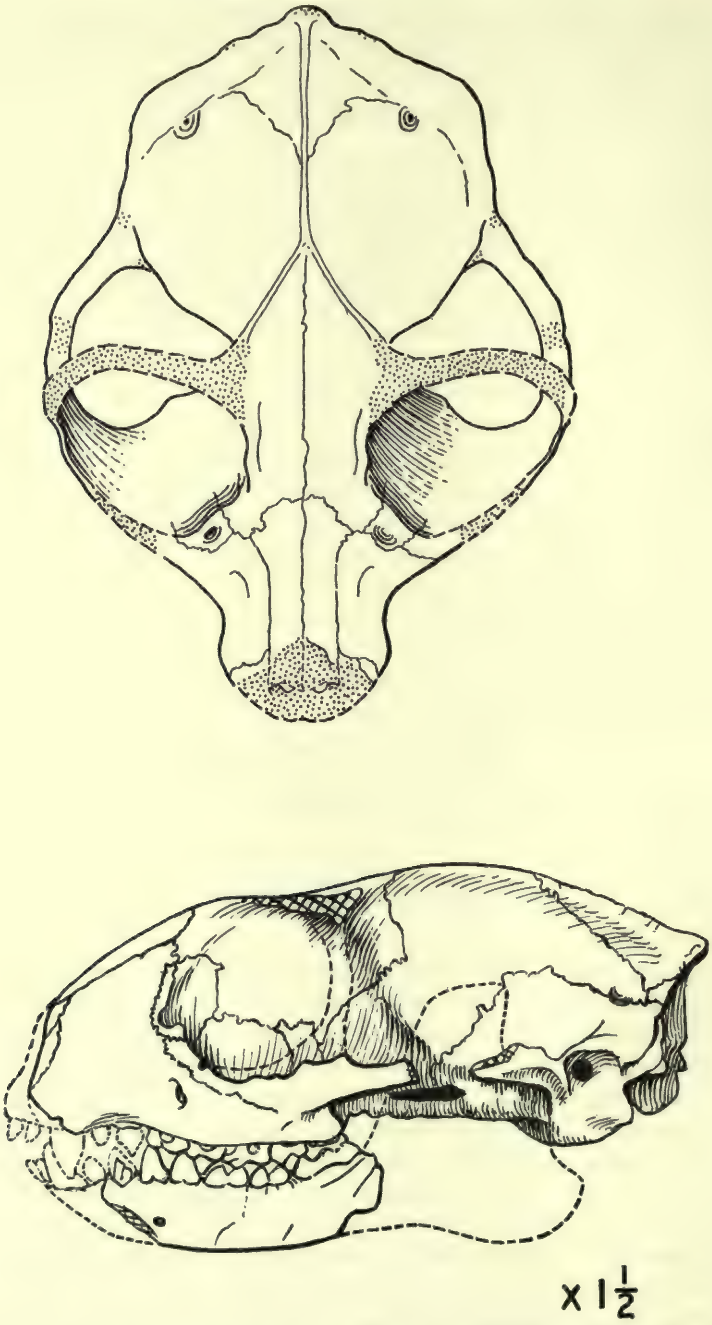


FIG. 2. Dorsal and lateral views of the skull of *Pronycticebus gaudryi* (Holotype), Hatching indicates broken surfaces, stipple missing parts. In dorsal view, right side restored from left.

found under the plaster, and with the much enlarged orbit indicated by the remaining median part of the orbital margin.[1] Living and fossil Primates with comparatively large orbits often have a slender post-orbital bar and a thin and flaring zygoma, as in *Galago* and *Necrolemur*. In fact, in some *Galago* species, the temporal base of the post-orbital bar in cross-sectional area is less extensive (when compared to total skull size) than is this area in *Pronycticebus*.

In view of the observed presence in *Pronycticebus* of both a frontal and a zygomatic base for the post-orbital bar, the large brain compared to *Adapis*, the complete absence of any evidence that other primates of the grade of advance seen in *Pronycticebus* lack the post-orbital bar, and the suggestion that enlarged orbits do sometimes correlate with relatively small frontal areas of attachment for the bar, no basis now remains for thinking that the bar was not continuous. Text-fig. 2 presents a conjectural restoration of its position.

Le Gros Clark (1934 : 20–27) noted most of the observable characters in the skull of *Pronycticebus* and discussed occurrences of many of these features in other Primates. The numerous new fossil primate specimens, which have been discovered or restudied since that time justify further comparison of some of these structures. Contrary to the current assumption *Pronycticebus gaudryi* is not a conservative form. With existence of a post-orbital bar in this species established, little remains to be seen in it that is particularly primitive for an Eocene primate. In fact, the expansion of the brain case, the large, forward-directed eyes and the short rostrum are all features that have been considered " advanced ".

Location of the lachrymal foramen, together with part of the lachrymal bone, outside the orbit in *Pronycticebus* was suggested as a difference from *Adapis* by Le Gros Clark (1934). However, a specimen of *Adapis magnus*, P U. 11481, indicates that in this species the position of the foramen and forward extension of the lachrymal may sometimes be about as in *Pronycticebus*. In Malagasy lemurs the lachrymal foramen typically lies further outside the orbit than in the foregoing, while in living lorisines, and the potto in particular, the position of foramen and lachrymal is about as in *Pronycticebus*, except for the smaller size of the lachrymal itself. *Necrolemur* (M.C.Z. 1179) and *Tarsius* have also a facial location of this foramen, but in *Smilodectes*, *Notharctus* and most platyrrhines this foramen clearly lies within the anterior orbital margin, as in pongids and man. In this character it would seem that *Adapis* and *Pronycticebus* approach more closely the living lemuroids than they do members of the Notharctidae and Anthropoidea. Forsyth Major (1901 : 151) concluded that the primitive condition for Primates is to lack a great facial expansion of the lachrymal. Shape and position of the foramen and lachrymal in *Pronycticebus* appear to be equivocal in relating it either to living lemurids or lorisids.

Rostrum

The comparatively foreshortened face of this primate is evident from the parts preserved. A vertical position of the premaxillo-maxillary suture (as well as the anterior recurving of the alveolar border around the canines) indicates that the missing anterior tip of the skull can hardly have been much longer than the conjectural reconstruction shown in Text-fig. 2. The sharp constriction in transverse diameter of the rostrum immediately posterior to the canines in *Pronycticebus* is not as distinct in living lemurs and is absent in *Adapis*. However, this feature can be seen in *Loris* and *Nycticebus*, and is one of the reasons why this skull is reminiscent of that of *Nycticebus coucang*.

---

[1] Relative to skull size *Pronycticebus* has larger orbits than most, if not all, other early Tertiary Primates. This may indicate nocturnal habits.

Dorsal Aspect of Skull

Cleaning of the skull has revealed sutures on the top of the brain case more clearly, and allows further comparison of this aspect of the skull in *Pronycticebus* with that of *Adapis*. Unlike *Adapis*, in *Pronycticebus* the posterior margins of the frontals extend on to the anterior part of the brain case. A sinus canal, near the posterior extremity of the parietal, is single in *Pronycticebus*, but in *Adapis parisiensis* it is multiple, as noted by Le Gros Clark (1934 : 22) and indicated by Stehlin's figures (1912). A large size for this canal has been said to be a primitive feature. After cleaning, sutures can be determined in *Pronycticebus* delimiting paired interparietals and (posterior to the sinus canal) small accessory ossicles (see Text-fig. 2). These bones have not been reported as occurring in *Adapis*. Taken as a whole the dorsal aspect of the brain case of *Adapis* does not closely resemble that of *Pronycticebus*. Such distinctions suggest that by the Middle or Late Eocene (the exact time range for both forms is uncertain) these two lemuroids had already diverged considerably. Such an assumption is reinforced by distinctions in other skull components, discussed above, such as the different shape of the muzzle, divergent character of the dentition, and difference in position and size of the orbits in these two Primates of the Quercy phosphorites. At present, it is probably better to retain them in the same family, as has been done by Hill (1953) and Piveteau (1957). Nevertheless, *Pronycticebus* and *Adapis* are as distinct morphologically as forms from the North American Eocene currently placed in different families, for example the notharctid, *Pelycodus*, and omomyid, *Ourayia* see Simons (1961*a* : 5).

Apart from the construction of the inside of the auditory bulla the basicranium of *Pronycticebus* was fully described by Le Gros Clark (1934). It will not be reconsidered in detail here. A possible alternative for an identification made by him (1934 : fig. 3) is that the foramen indicated as the hypoglossal canal may be the inferior petrous sinus.

On obtaining permission to examine the interior of the auditory bulla it was determined that the ectotympanic is not tubular, thus completely confirming, in this regard, Le Gros Clark's thesis that this primate is not a tarsioid. It is noteworthy that the annulus lies very near the external auditory meatus and, unless it has been displaced, appears to be fused with the bulla wall in its posterior third, just internal to the posterior rim of the external meatus. From this point the annulus arches inward and downward, so that its ascending anterior limb lies some distance from the antero-lateral wall of the bulla. Near the ventral extremity of the ring (and external to it) is a shelf on the lateral bulla wall for the support of the annulus membrane. Compared to that of *Adapis* this shelf is quite small. Hill (1953 : 113) figures a dissection of the auditory bulla of *Loris tardigradus* which indicates only slightly greater reduction of the annulus. The position of the tympanic ring in *Pronycticebus*, close to the external meatus, is an additional indication that Grandidier may have been nearer the truth than has sometimes been thought, when he suggested an affinity between this species and the modern lorises.

Dentition

It was principally because of the somewhat enlarged brain and generalized characters of the dentition (resembling teeth of *Anchomomys* a supposed tarsioid), that such students as Stehlin (1916 : 1422), Gregory (1922) and Abel (1931 : 186) referred this primate to the tarsioids. Founding his conclusions principally on characters of the skull Le Gros Clark demonstrated that this primate cannot be considered a tarsioid. However, it may not have been sufficiently stressed that the dentition also, although unspecialized, is not *Tarsius*-like. Some principal reasons why this dentition does not indicate tarsioid relationships are as follows :

The cross-sectional area of the upper canine base is considerably greater relative to adjacent teeth than it is in *Tarsius* while in necrolemurines the upper canine is even smaller proportionately than in *Tarsius*. Tarsiids, with the possible exception of *Nannopithex*, lack the P^1 present in *Pronycticebus*. The latter primate, like *Adapis*, *Protoadapis*, *Anchomomys* and *Progalago*, has two-rooted second premolars above and below, while in tarsiines, these teeth are always single-rooted. In configuration of the remaining teeth *Pronycticebus* closely resembles *Protoadapis*, but differs from it dentally in having a less well-developed lingual cingulum on the upper molar protocone, and a more reduced M_{2-3} paraconid. However, these are rather slight distinctions, known to be variable in other primate species.[1] Otherwise, these two forms agree in such features as the absence of mesostyles, and of a distinct hypocone on M^3 (although it is well developed on M^1 and M^2). Also, they are closely similar in proportion and size. It is just possible that better specimens might even show that species of these two types of Primates are not separable generically. Unlike tarsioids, *Pronycticebus* has, as Simpson (1940 : 202) remarks (with reference to *Caenopithecus*) " open trigonids and the peculiar mode of paraconid reduction so characteristic of *Adapis* and its close allies and unknown among any forms of really probable tarsioid affinities ".

Cranial Proportions

A logarithm of ratio diagram (Text-fig. 3) indicates graphically the close similarity in linear proportions between *Pronycticebus* and *Nycticebus* and in contrast to those of an early Cenozoic lemuroid species *Adapis magnus*? and a Recent Malagasy lemur.[2]

---

[1] Even in *Protoadapis*, as is indicated by isolated upper molars from the Geiseltal coals at Halle, the lingual protocone cingulum of the upper molars is sometimes incomplete, as it also is in *Pronycticebus*.

[2] Measurements indicated in Text-fig. 4 are as follows : (1) Transverse diameter from mid-line of skull to greatest flare of zygomatic arch. (2) Length of skull, from posterior margin of canine to anterior margin of foramen magnum. (3) Length of skull from posterior margin of canine to posterior extremity of skull. (4) Length of dentition from anterior face of canine to posterior edge of M^3. (5) Greatest transverse width of dentition. (6) Greatest transverse diameter of the cranium. (7) Least post-orbital diameter of skull. (8) Length from posterior margin of the canine to end of hard palate. (9) Length from anterior margin of canine to point of least post-orbital diameter. (10) Length from point of least post-orbital diameter to posterior tip of skull. (11) Greatest diameter of orbit from base of post-orbital bar to opposite rostral orbital margin. (12) Greatest transverse diameter across auditory bullae. (13) Greatest transverse diameter across canines. (14) Least transverse diameter of muzzle across upper second premolars.

The major differences between *Nycticebus* and *Pronycticebus* are in plots 4, 7, and 8. Measurement number 4, the length of the upper teeth might be expected to be less in *Nycticebus* as its dental formula is more reduced, and the same would apply to measurement number 8, the approximate length of the hard palate. Measurement number 7, the least post-orbital diameter of the skull (much smaller in *Pronycticebus*) is a primitive feature, correlated with a comparatively unexpanded brain, and is common to all Eocene lemuroids. In the remaining measurements *Pronycticebus* falls within (or very close to) the range of size variation of a small sample of the living lorisid *Nycticebus coucang* (10 individuals).

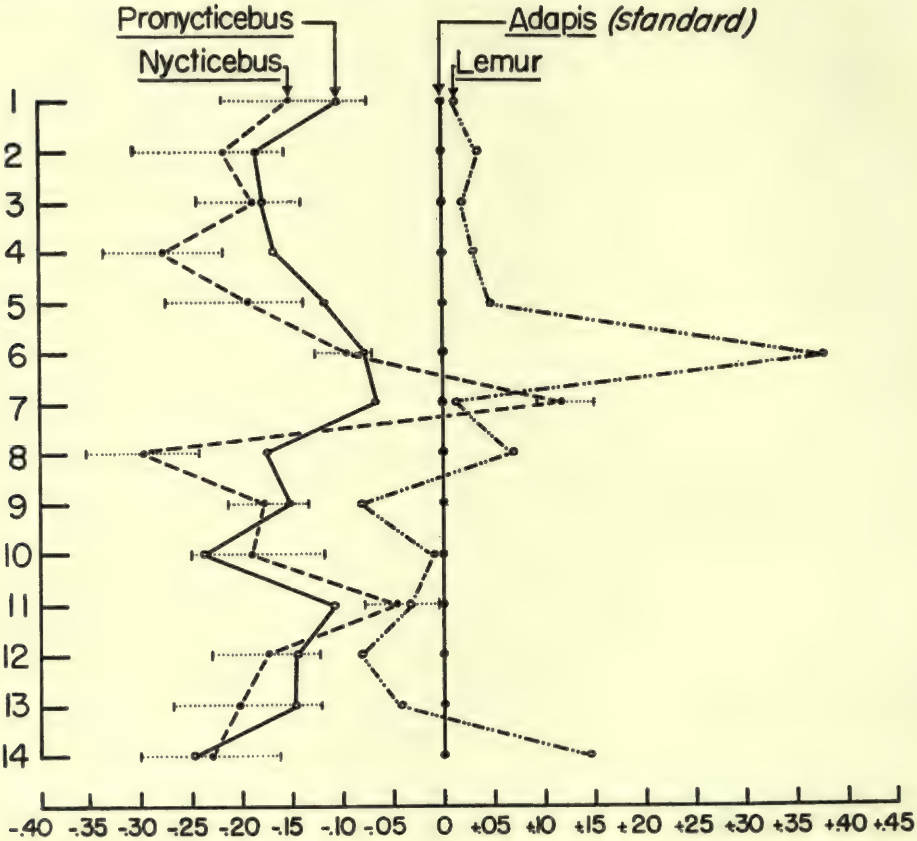


FIG. 3. Logarithm of ratio diagram comparing cranial proportions in four prosimians; *Adapis* (standard). Mean, and extremes of range are indicated for a sample of ten *Nycticebus coucang*.

CONCLUSIONS

Perhaps all the above-mentioned similarities are due to parallelism produced by similar adaptations in *Pronycticebus* and lorises, but such a view appears to be rather strained. A more likely conclusion is that *Pronycticebus* does have some relationship to the radiation which produced extant Lorisiformes. Nevertheless, because of many primitive structures also shared with the contemporary *Adapis* and *Protoadapis* it seems best not to remove this genus from the Adapidae, at present.

IV. THE TAXONOMIC POSITION OF *ANCHOMOMYS* STEHLIN (1916)

(Text-fig. 4)

This rather small primate, originally described by Stehlin (1916) occurs in deposits ranging from early Lutetian to early Ludian age in Europe. Four species have been proposed, differing little in known parts except for size. Taxonomic placement of this genus has varied considerably. Abel (1931 : 175) and others considered it a tarsioid, but Simpson (1940 : 202) quite correctly pointed out that such an assignment was most improbable. Of European Eocene lemuriforms the closest dental resemblances to *Anchomomys* are to be seen in *Pronycticebus* and *Caenopithecus*, but because of a common simplicity in cusp pattern their similarities can, perhaps, be over-emphasized. In some respects these three genera also resemble *Adapis*, particularly in type of paraconid reduction, but all three differ from *Adapis* in having M_3 hypoconulid much more distinctly set off as a separate lobe from the hypoconid. They also lack the bicusped ectoloph of P^4 and continuous lingual upper molar cingula seen in *Adapis*.

For *Anchomomys* the closest dental resemblances appear to be with a Miocene lorisiform of Kenya, *Progalago*. In fact, in spite of the differences in time and place of occurrence of the species belonging to these two genera, some of the European Eocene forms, particularly *Anchomomys quercyi*, can hardly be distinguished generically, on the basis of parts preserved, from *Progalago dorae*. Species of these genera also overlap as far as size is concerned and similarities in the lower molars are particularly striking. Both exhibit reduced paraconids, well-developed entoconids, a large M_3 hypoconulid, with remaining molar cusps of closely corresponding shape and situation relative to one another. Both these prosimians also display in the major molar cusps a fairly distinctive angular or pyramidal form.

The upper molars of *Anchomomys* are quite like those of *Progalago* although in some, but not all, species of *Anchomomys* the paraconule and metaconule are more distinctly developed. In *Progalago dorae* and *Anchomomys quercyi* the latter two cusps are absent, see Text-fig. 4. These two species are alike in having a subquadrate M^1 with large hypocone, more triangular M^2 with smaller hypocone and lack a distinct M^3 hypocone, see Text-fig. 4 ; Le Gros Clark (1956, pl. 1) and Stehlin (1916, figs. 327, 328, 332). Moreover, at least one specimen of *Progalago dorae* (Le Gros Clark & Thomas, 1952, pl. 3, fig. 9) shows that in this species the P^2 was a much elongated and two-rooted tooth. If the same applies to the maxilla of *Anchomomys quercyi* figured by Stehlin, and shape of the anterior alveoli strongly indicates this possibility, then the upper dental formulae of both species are identical, at least from the canine posteriorly.

Perhaps the best preserved skull of *Anchomomys* is that of the unnumbered holotype of *Anchomomys latidens* (now in Paris) described by Teilhard (1921 : 13) from the Quercy phosphorites and identified as " Rossignol Collection 1893 : 11 ". The specimen is much broken and distorted, but careful preparation could probably expose more of the cranial anatomy. As in *Pronycticebus* and *Progalago* there is a single large infra-orbital foramen above P^4. The anterior root of the zygoma appears to arise about M^2, and through this anterior root opens to the rear a relatively large posterior infra-orbital canal. On the antero-dorsal surface posteriorly converging temporal ridges are evident, but the dorsal insertion of the post-orbital bar cannot be distinguished. Between these temporal ridges, there is a broad depression, appearing rather as does this area in *Pronycticebus*. An apparently distinctive feature of *Anchomomys latidens* is the character of the surface of the temporal bone which is covered by numerous minute foramina, a condition certainly not to be seen (to this extent, if at all) in *Adapis* or *Necrolemur*. At the back of this skull are well-developed nuchal crests. These are typical of Eocene Primates and their presence is consistent with the retention of similar strong ridges in this position in *Progalago*.

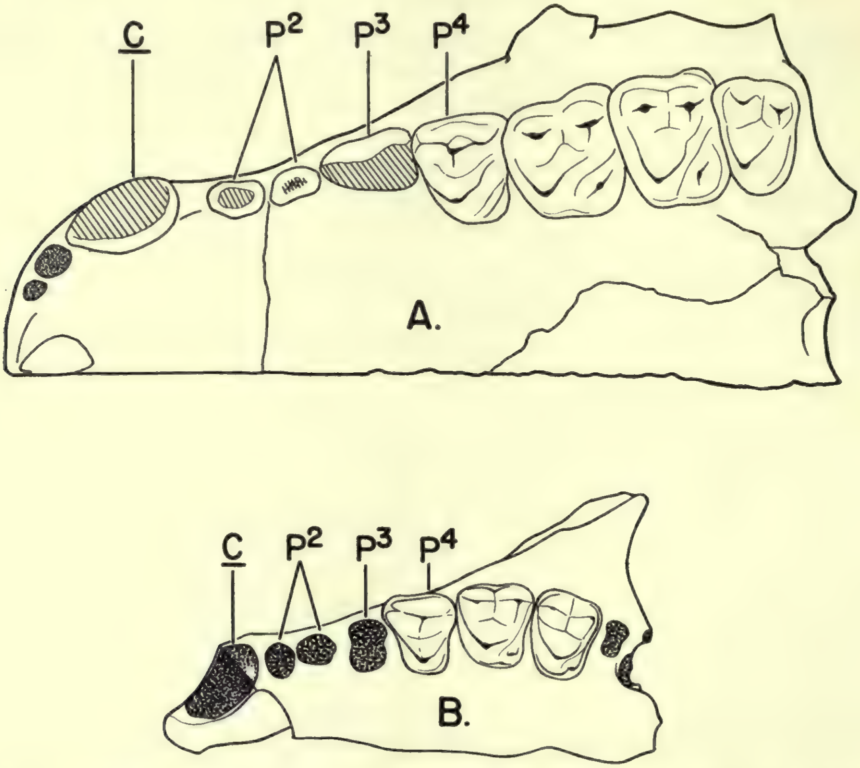


FIG. 4.—Comparison of upper dentition in *Anchomomys* and *Progalago*. A. *Progalago* sp.. [Diagram after Le Gros Clark, 1956, pl. 4, fig. 1.] Right maxilla, reversed, ×7·5 approx. B. *Anchomomys quercyi*. [After Stehlin, 1916, fig. 332.] ×7·5 approx.

Taxonomic Position

Stehlin (1912 : 1426) tended to favour the idea that *Pronycticebus* and *Anchomomys* have about the same relationship to the Galagidae [" Nycticebiden "] as *Adapis* has to the lemuriform lemurs, but remarked that until the position of the carotid foramen and situation of the extotympanic was revealed for one of these Primates their taxonomic position would remain uncertain. Now that the annulus of *Pronycticebus* is known to show a possible foreshadowing of the condition seen in lorisiform Primates, Stehlin's analysis is strengthened. The subsequent placement of these two genera among the tarsioids, proposed for *Anchomomys* by Teilhard (1921), and for both *Pronycticebus* and *Anchomomys* by Gregory (1922) and Abel (1931) can now be seen to have marked a step backward in determination of their relationship to other prosimians.

Teilhard, although stressing tarsioid relationships for *Anchomomys latidens*, did however remark (1921 : 16) : " Tout au plus pourrait-on le rapprocher des *Galago* pour le développment de l'hypocône et la tendance à la molarisation de P 4 . . . ". This observation is important taxonomically because the fourth upper premolar in species of the genera *Anchomomys*, *Progalago* and *Galago* has an interesting similarity in basic plan, in addition to the other features of resemblance between these genera mentioned above. The view that these forms were tarsioids was rejected by Simpson (1940) after Le Gros Clark's study of the cranial anatomy of *Pronycticebus*, but since then their position among the non-tarsioid Prosimii has remained uncertain.

The very close dental relationship between *Anchomomys* and *Progalago*, and the similarities which the latter in turn has with living lorisoids reinforce the idea that this phylum can now be traced back with a fair degree of accuracy as far as the European Middle Eocene.

V. RELATIONSHIPS OF EARLY TERTIARY LEMUROID PRIMATES

The Concept of " Lemuroid " Primates

One objective of the research reported here and in Simons (1961) has been to determine whether tarsier-like and lemur-like Primates can be distinguished in the early Cenozoic. For at least one subfamily of this period, Necrolemurinae, a definite relationship with *Tarsius* is indicated. Most remaining Paleocene and Eocene Primates have (or should have) been termed " lemuroid " in the past. A great many fossil genera have consistently been classified as tarsioid when there is no basis, in known parts, for so doing. If one examines the better known lemuroid Primates they seem to be of four general kinds, as follows :

(1) Species on the border-line between Primates and Insectivora as these orders are currently understood, of the families :

Amphilemuridae
Microsyopidae
Apatemyidae

(2) Specialized Primates of early extinction. Forms too specialized dentally to be near ancestral lines of later stocks :

Families :
- Plesiadapidae
- Carpolestidae
- Anaptomorphidae [in part]
- Paromomyidae [=Phenacolemuridae, in part]

(3) Relatively generalized groups that could be near the ancestry of some living families, but which show no convincing evidence of having reached a tarsioid, or higher, grade of advance.

Families :
- Adapidae
- Notharctidae

(4) Generalized Primates, possibly close to the stocks which gave rise to living groups, but which are not well enough known to indicate their grade of advance.
- Omomyidae
- perhaps some [paromomyids and anaptomorphids]

Past usage has roughly equated the term lemuroid with at least some members of each of the four groups of extinct families listed above. Such usage implies, however, that all these types can be assigned to the Lemuridae, which is not the case. On the other hand, it is surely valid to assume that the ancestral stocks of all the groups which have advanced beyond the lemur-like state (represented today by tupaiids and lemurids) went through such a level of advancement, and consequently their ancestors of the early Cenozoic can correctly be called lemuroid or lemur-like. Obviously then, among fossil forms that are distinctly lemuroid may be found ancestors of the more advanced Primates : tarsioids, and anthropoids. Some members of the above families do foreshadow tarsioids. For instance, *Navajovius* of the Tiffanian Paleocene of Colorado and *Teilhardina* of the Sparnacian Eocene of Belgium, both exhibit interesting dental resemblances to the European Middle Eocene tarsiid, *Nannopithex*, while the only skull with advanced (or tarsioid) features ever discovered in North America (*Tetonius* ; A.M.N.H. 4194) also possesses upper molars that, together with a general similarity of detail, share with those of *Nannopithex* an unusual feature, the nannopithex-fold. At present these four genera are assigned to three different families, viz.

Navajovius and *Teilhardina* .	Omomyidae (Simpson, 1940 : 208)
Nannopithex	Tarsiidae (Simons, 1961 : 61)
Tetonius	Anaptomorphidae (Gazin, 1958 : 73)

Dental variation among these primates is not as great as their assignment to different families implies, being in most ways far less than seen in the Malagasy family Lemuridae. Yet, until better cranial remains are known for some omomyids, paromomyids and anaptomorphids it will remain difficult to judge whether or not these groups show the same definite indications of tarsioid relationships in their osteology than they do in their dental anatomy. All these most interesting Primates fall within the fourth group listed on p. 24. In regard to the first three groups primatologists are on safer ground, for they are either so primitive dentally that tarsioid relationships cannot be considered or they are known from skulls that show no convincing tarsioid features. In the broadest sense it appears reasonable to call these forms lemuroid, and it is with them that the following paragraphs will be concerned.

Border-line Primates

Amphilemuridae

This family, proposed by Heller (1935) for the reception of *Amphilemur eocaenicus* from the Middle Eocene deposits of the Geiseltal, has recently been assigned to the Erinaceoidea (Insectivora) by McKenna (1960 : 58). To this subfamily McKenna also assigns, among others, the following North American Paleocene and Eocene genera : *Entomolestes*, *Macrocranion* and *Sespedectes*. As far as Primate classification is concerned, this procedure is not likely to improve the taxonomy of the genera involved, for the type of *Amphilemur* cannot be located at Halle, and if lost makes an unsatisfactory choice as the type genus of a subfamily known otherwise only in the New World, and to which it may not belong. Both Simpson (1945) and Hill (1953) refer *Amphilemur* to the Adapidae, *incertae sedis*. In its poorly-known state, now entirely dependent on Heller's text and figures, there is little basis for placing it elsewhere. In *Adapis parisiensis* the lower canine is often very small and otherwise the antemolar teeth exhibit gradual and nearly unbroken size-decreases from back to front, which is not unlike the size sequence of these lower teeth in *Amphilemur* and which shows that the same general kind of tooth proportions seen in *Amphilemur* can occur in a primate.

Microsyopidae

McKenna (1960 : 76) has re-defined this family so as to include the following genera : *Microsyops*, *Craeseops* and *Cynodontomys*. His view, that this family belongs among the Primates appears to have sound justification. He is of the opinion that the nearest affinities of the Microsyopidae, as re-defined by him, are with the more primitive plesiadapids of North America. Moreover, he remarks (1960 : 78, 79) while discussing Microsyopidae :

> " Recently Hürzeler (1948*a*, pp. 343–356) has described a new genus and species, *Alsaticopithecus leemanni*, from the Lutetian of Alsace, based on excellent dental material. The animal was placed in the Primates *incertae sedis*. *Alsaticopithecus* appears to me to be a microsyopid . . . As Hürzeler notes, the genus is indeed primatelike. Thus *Alsaticopithecus* has a bearing on the problem of microsyopid origins. The genus is an interesting extension of the known statigraphic and geographic range of microsyopids."

In view of this assignment of *Alsaticopithecus*, taken together with what is now known of microsyopid anatomy, including cranial material, soon to be reported on by McKenna, Hürzeler's conjecture that this form has significant dental resemblances to Anthropoidea is no longer tenable.

Apatemyidae

The series of genera now assigned to this family were first clearly distinguished from plesiadapids by Jepsen (1934). Although they are retained provisionally in the order Primates by Gazin (1958), research on the basicranium reported by Hürzeler (1949 : 485) indicates that this group is almost certainly not to be referred to the Primates, as the order is now defined. Notwithstanding this, the apatemyids may have had their origin in the same eutherian stock from which the Primates arose—a conclusion which is indicated principally by molar-pattern resemblances. They certainly have no close connection with Paleocene-Recent Primates and will not be considered further here.

Specialized Lines of Early Extinction

A number of divisions of the order of family and subfamily status, which became extinct before the end of the Eocene, exhibit such pronounced dental specializations that it is clear they could not be near the ancestry of any living Primate species. Of these, the carpolestids are the least well understood, but conformation of the fourth lower premolar alone (elongate and saw-like) removes them from consideration as ancestral to surviving lines. The same applies to plesiadapids, and to *Phenacolemur*[1] because of the marked reduction of their anterior dentition. Even so, *Plesiadapis* is of interest because of its geographical distribution. Species of this genus are known from the late Paleocene of both Europe and North America. This occurrence demonstrates that climatic conditions as well as the requisite land-bridges, allowing not only other mammals but prosimians to communicate between these two continents then existed, and helps to explain the presence of omomyids, microsyopids and possibly other primate families, in both continents in the early Eocene.[2]

Among the plesiadapids, carpolestids, and paromomyids the cranial and postcranial anatomy is poorly known except in two species of *Plesiadapis*. The limb bones of *Plesiadapis* studied by Simpson (and greatly amplified by undescribed specimens recently collected by Russell in the Cernay Paleocene deposits near Rheims in central France) are primitive, but can be spoken of as lemur-like. Russell (1960) briefly reported on a remarkably well-preserved skull of *Plesiadapis* from the Cernay region. This is the oldest primate skull yet to be described. The skull of *Plesiadapis* is very broad, flat, with a small brain-case, while the premaxillaries are enormously expanded and make up most of the muzzle. Elsewhere, among Primates such expanded premaxillaries occur only in the Madagascan lemur *Daubentonia*. However, a relationship with the latter is excluded by the presence in *Plesiadapis*, but not in *Daubentonia*, of a tubular ectotympanic element. Finally, it is clear that in *Plesiadapis* there is no post-orbital bar, nor any indication of post-orbital processes.

---

[1] Here regarded as a paromomyid, following McKenna (1960 : 70).

[2] Basically all living prosimians are tropical forest dwellers. Uniformitarian reasoning would suggest that their early Cenozoic forerunners were also warm-climate animals.

From this feature of the Cernay *Plesiadapis* skull it must be concluded that the basal stock of the order lacked the post-orbital bar, although it occurs in all other undoubted Primates (for which this part of the skull is known) with the single exception of *Anagale* from the Oligocene of Mongolia.

The families Anaptomorphidae and Paromomyidae are known only from North America. In terms of present knowledge, they include the most likely candidates for a relationship with the rise of tarsioids and of surviving higher Primates, possibly by way of containing forms ancestral to the omomyids. Regrettably members of these families, with the exception of *Tetonius*, are known only from dentitions, and consequently, little can be said as to whether they are lemur-like or tarsier-like. The same is true for omomyids. Nevertheless, dental analogies suggest that some of the species referred to these families were at least transitional to the tarsioid grade and such an assumption is further indicated by the large, forward-directed orbits and expanded brain of *Tetonius*.

VI. REVISED CLASSIFICATION OF EUROPEAN EOCENE PRIMATES

Revisions included here, in Simons (1961), and in a number of other works published since Simpson (1945) now make it possible to assign taxonomically certain European early Cenozoic Primates formerly listed by Simpson as *incertae sedis*, as well as to transfer others for which a better placement can be supported. The most recent extensive treatment of these forms is by Hill (1953, 1955), but Hill's taxonomy is clearly synoptic and no revision of fossil prosimians is included in these works. The following section, therefore, attempts to bring the classification of the fossil Primates of Europe up to date.

Genera to be considered here are listed in Simpson (1945) as follows :

Plesiadapidae :
    Megachiromyoides Weigelt, 1933. M. Eoc.; Germany.
Adapidae *incertae sedis* :
    Caenopithecus Rütimeyer, 1862. M. Eoc.; Switzerland.
(?) PROSIMII of uncertain infraorder or family :
    Ceciliolemur Weigelt, 1933. M. Eoc.; Germany.
    Europolemur Weigelt, 1933. M. Eoc.; Germany.
    Megatarsius Weigelt, 1933. M. Eoc.; Germany.
    Microtarsioides Weigelt, 1933. M. Eoc.; Germany.

Two additional Eocene Primates from Europe described by Hürzeler (1946, 1947) are also discussed in the following pages.

Gesneropithex peyeri Hürzeler, 1946. M. Eoc.; Switzerland.
Alsaticopithecus leemanni Hürzeler, 1947. M. Eoc.; Alsace.

Inasmuch as the European plesiadapids, and a specimen from the Walbeck Paleocene of Germany, referred to *Phenacolemur* by Weigelt (1947) but of uncertain generic and familial assignment are currently under study by others they are not discussed here in detail. These groups are, however, indicated in Text-chart 1, in

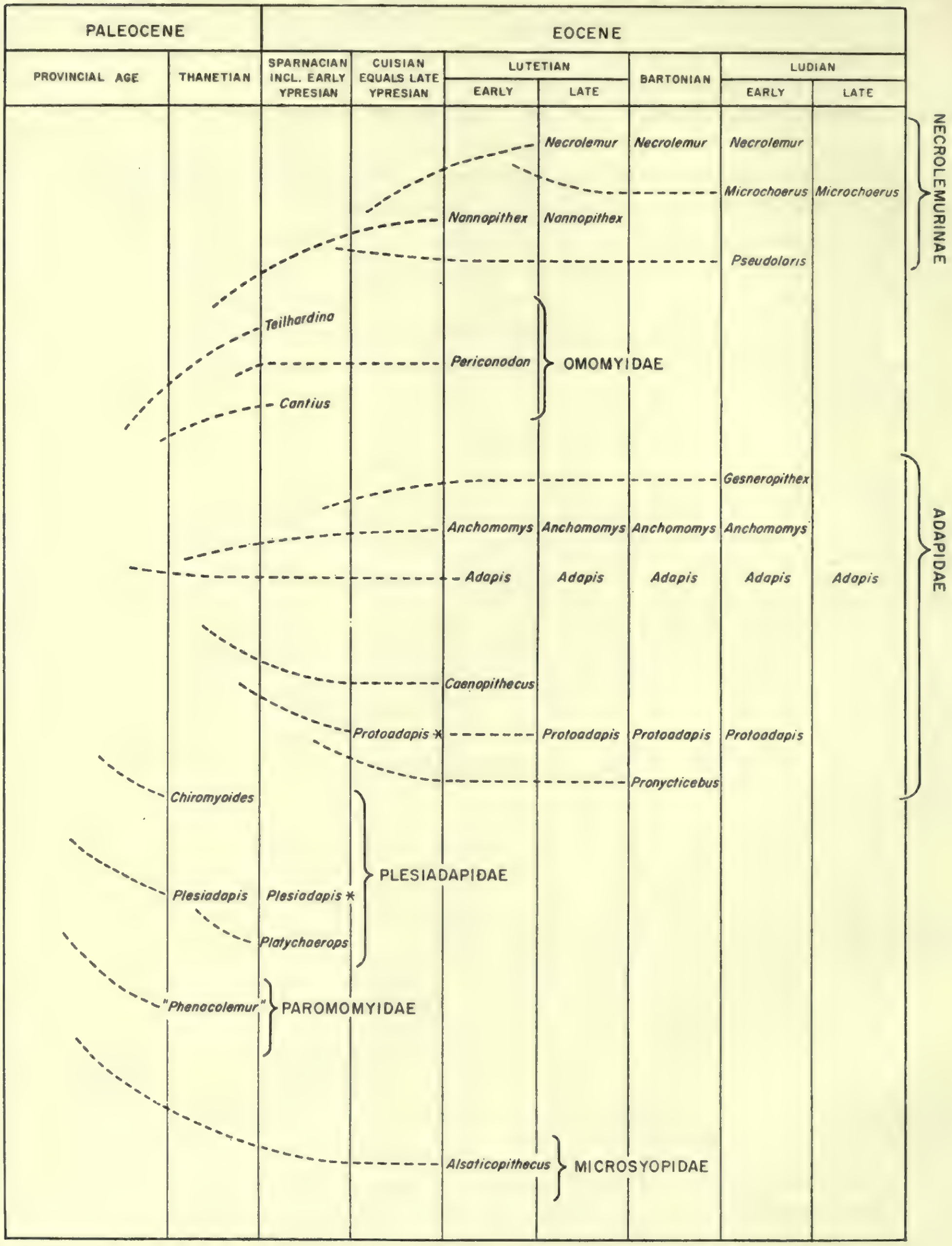

PALEOCENE
EOCENE
PROVINCIAL AGE
THANETIAN
SPARNACIAN INCL. EARLY YPRESIAN
CUISIAN EQUALS LATE YPRESIAN
LUTETIAN
EARLY
LATE
BARTONIAN
LUDIAN
EARLY
LATE
Necrolemur
Necrolemur
Necrolemur
Microchoerus
Microchoerus
Nannopithex
Nannopithex
Pseudoloris
NECROLEMURINAE
Teilhardina
Periconodon
OMOMYIDAE
Cantius
Gesneropithex
Anchomomys
Anchomomys
Anchomomys
Anchomomys
Adapis
Adapis
Adapis
Adapis
Adapis
ADAPIDAE
Caenopithecus
Protoadapis *
Protoadapis
Protoadapis
Protoadapis
Pronycticebus
Chiromyoides
Plesiadapis
Plesiadapis *
Platychaerops
PLESIADAPIDAE
"Phenacolemur"
PAROMOMYIDAE
Alsaticopithecus
MICROSYOPIDAE

CHART I

Temporal occurrence of early Cenozoic European primate genera indicating approximate interrelationships. (* Occurrence in this horizon dubious.)

CHART I.

which temporal occurrences and approximate interrelationships of all European early Tertiary Primates are shown.

Megachiromyoides

Since *Megachiromyoides* is frequently referred to in the literature as a primate, it should be emphasized that Stehlin & Schaub (1951 : 21) stated that it is a rodent, assignable to the genus *Aeluravus*. A recent examination, by the writer, of the holotype of " *Megachiromyoides* " from the Geiseltal Brown Coals (described by Weigelt, 1933) has confirmed the view that this form cannot possibly be a plesiadapid.

Caenopithecus

This interesting primate from Middle Eocene (Lutetian) deposits near Egerkingen, Switzerland was originally described by Rütimeyer (1862). Stehlin (1916) discussed the species further and figured a mandible which shows only one incisor alveolus on either side. He stated that his material indicated the same lower dental formula as in *Tarsius*, and noted other advanced features including the loss of the first upper and lower premolars, and a short rostrum.

Corroboration of Simpson's placement (1940) of this primate among adapids can be drawn from its similarities with the Lutetian species *Protoadapis klatti*. Principally *Caenopithecus* differs from *Protoadapis* in showing more reduced molar paraconids, in the possession of distinct mesostyles and in having less well-developed upper molar lingual cingulum. *Protoadapis* also exhibits a more distinct P^3 protocone. In spite of these generic differences, however, *Caenopithecus* and *Protoadapis* are, in upper and lower dental conformation, in dental formula and in what is known of the skull, much closer to each other than either is to *Adapis*, but (in different ways) both exhibit some features of resemblance to a species of the latter genus.

Stehlin (1916 : 1319) remarked that knowledge then available of *Caenopithecus lemuroides* indicated affinities with *Protoadapis* and *Pelycodus* and this view has been strengthened by the better material of *Protoadapis klatti* now known. *Protoadapis* and *Caenopithecus* agree in possessing the following features, some of which are unknown among other European Eocene Primates : Long and large canines (above and below)—not very procumbent ; $P1/1$ absent and replaced by diastema ; P_3 higher than P_4 ; metaconule of upper molars lacking but distinct paraconule present ; well-developed hypocones on M^{1-2} only ; upper molar cingula (labial and lingual) well defined and in some individuals continuous across lingual base of protocones ; similar proportions in lower molars.

Common possesssion of pronounced upper molar cingula, absence of a distinct P^3 protocone and near identity in overall proportions of the lower molars between *Caenopithecus* and *Adapis parisiensis*, tend to link species of these two genera as well. Weigelt noted a slight mesostyle on the M^2 of *Protoadapis klatti* (also in agreement with *Caenopithecus*) and expressed the view that his Brown Coal species was closer to *Caenopithecus* than to *Adapis*. Moreover, his illustration of the skull of *P. klatti* (1933, pl. 6, fig. 4) indicates a vertically deepened anterior base for the zygomatic arch, as in *Caenopithecus lemuroides*. One further similarity between these two types of Primates is the possible loss (reported for species of both genera) of all but one pair of lower incisors. Because of the low angle at which the anterior alveolar border of the mandible of *Caenopithecus* (Basel Eh. 733) from which this was deduced, is broken off, the possibility remains that there were more incisors below. In some specimens of *Adapis parisiensis* in the Paris Museum, where this margin is broken off in a similar way, the incisor alvoli are entirely missing. If these were the only known specimens of *A. parisiensis* its lower incisor formula would be equally uncertain. The exact number of lower incisor pairs in given Eocene primate species can seldom be stated categorically. Both *Caenopithecus* and *Protoadapis* could have had two pairs of these teeth, but present evidence is not adequate to prove that they did.

A further note of some interest regarding *Caenopithecus*, and the nature of true hypocones and pseudohypocones, is provided by a specimen of this primate at Basel (Eh. 727) which shows both kinds of hypocone formation in one individual. The retention of both of these patterns in this dentition suggests that a latency for producing pseudohypocones, as in the line leading to *Notharctus* as well as for true hypocone production in *Adapis*, probably existed in the ancestral adapid-notharctid stock.

Periconodon

The genus *Periconodon* was established by Stehlin (1916) for a species " *helveticus* " which had been assigned by Rütimeyer (1891 : 115) to the North American genus *Pelycodus*. Like most *Caenopithecus* materials the type of *Periconodon helveticus* came from Middle Eocene deposits near Egerkingen, Switzerland. Apparently no additional specimens referable to this genus have been discovered since Stehlin's discussion.[1] The individual illustrated by Stehlin (1916, pl. 22 fig. 3), which preserves P^3 and M^{1-2} shows a distinctive pericone on the antero-internal base of M^{1-2} protocones. Since a pericone sometimes occurs here in *Omonys* (see Gazin, 1958, pl. 6, figs. 3 4) but not elsewhere among early Tertiary Primates, and because omomyids are known to have been present in the European Eocene fauna, the provisional reference of *Periconodon* to this family seems advisable. Furthermore, the small size of the species and general conformation of the teeth does not suggest adapid or notharctid affinities.

Ceciliolemur and *Microtarsioides*

Ceciliolemur is now considered by Matthes (1957), and by others, to be an insectivore, primarily because it seems to have had dermal spines. Recent examination of the holotypes of *Ceciliolemur*, G.P.I.H. 4237, and of *Microtarsioides*, G.P.I.H. 4235, both from the Geiseltal Brown Coals of Cecilia mine, locality Leichenfeld II, indicates strongly that they belong to the same species. Cheek teeth do not survive in either specimen, so dental formula and affinities cannot be determined. Moreover, the condition of bones and of eruption of lower teeth indicate that both are very young individuals, perhaps pre-natal. No basis remains for referring either of these specimens to the Primates. It is a remarkable accident of fossilization that either of these very delicate specimens were preserved, considering that the body excluding the tail, in both cases, is only about 4 cm. long. Locality data indicates recovery from the same place, and possibly they are from the same " litter ".

---

[1] Heller (1930) and Weigelt (1933) both mention the presence of isolated upper molars of this Primate in the Geiseltal Brown Coals. These teeth do not belong to *Periconodon*, but are those of a larger Primate from which the enamel has been resorbed. What remains of the cusp bases suggests their reference to *Protoadapis klatti*.

Europolemur and *Megatarsius*

As discussed above (pp. 13, 14) these primate genera are junior synonyms of *Protoadapis*.

Alsaticopithecus

The species *Alsaticopithecus leemanni* Hürzeler (1947) can be assigned to the family Microsyopidae, as re-defined by McKenna (1960 : 76), see p. 25.

Gesneropithex

Gesneropithex peyeri Hürzeler (1946) is based on a lower jaw containing P_4–M_2 and one second upper molar collected in Ludian deposits near Bösgen, Switzerland. The lower teeth differ from *Alsaticopithecus* and resemble such adapids as *Anchomomys*, in that M_{1-2} lack distinct hypoconulids. Moreover, conformation of the upper second molar is within the general range of variability of species now assigned to the Adapidae. M^2 is most similar in size and cusp pattern to those of *Anchomomys latidens*, but wear obscures some of its features. *Anchomomys* and *Gesneropithex* also agree in one rather unusual feature of M^2 ; both have a strong anterior crest running from the metaconule to the metacone. Presence of an upper molar mesostyle in *Gesneropithex* is in agreement with *Caenopithecus*. It seems reasonable to assume that *Gesneropithex peyeri* can be referred to the Adapidae (s.s.).

REVISED CLASSIFICATION[1]

Order *PRIMATES*
Suborder PROSIMII
Family TARSIIDAE Gray, 1870
Subfamily NECROLEMURINAE Simpson, 1933

MICROCHOERUS Wood, 1844
Synonyms—*Microchaerus* Forbes, 1894
Necrolemur : Filhol, 1880 (in part)

Microchoerus erinaceus Wood, 1844
Microchoerus edwardsi (Filhol, 1880)
Synonym—*Necrolemur edwardsi* Filhol, 1880
Microchoerus ornatus Stehlin, 1916

---

[1] Since a revision of the European plesiadapids is currently being undertaken by Russell at the Paris Museum they have been omitted from this classification.

NECROLEMUR Filhol, 1873
Necrolemur antiquus Filhol, 1873
Necrolemur zitteli Schlosser, 1887

NANNOPITHEX Stehlin, 1916
Synonyms—*Necrolemur* Chantre & Gaillard, 1897
Pseudoloris : Weigelt, 1933
Nannopithex filholi (Chantre & Gaillard, 1897)
Synonyms—*Necrolemur filholi* Chantre & Gaillard, 1897
Nannopithex pollicaris Stehlin, 1916
Nannopithex raabi (Heller, 1930)
Synonyms—*Pseudoloris abderhaldini* Weigelt, 1933
Necrolemur raabi Heller, 1930

PSEUDOLORIS Stehlin, 1916
Synonym—*Necrolemur* : Filhil, 1889
Pseudoloris parvulus (Filhol, 1889)
Synonym—*Necrolemur parvulus* Filhol, 1889

Family OMOMYIDAE Gazin, 1958

TEILHARDINA Simpson, 1940
Synonym—*Omomys* Teilhard, 1927
Teilhardina belgica (Teilhard, 1927)
Synonym—*Omomys belgicus* Teilhard, 1927

CANTIUS nov. gen.
Synonym—*Protoadapis* : Cooper, 1932
Cantius eppsi (Cooper, 1932)
Synonym—*Protoadapis eppsi* Cooper, 1932

PERICONODON Stehlin, 1916
Synonym—*Pelycodus* Rütimeyer, 1891
Periconodon helveticus (Rütimeyer, 1891)
Synonym—*Pelycodus helveticus* Rütimeyer, 1891

Family ADAPIDAE Trouessart, 1879

ADAPIS Cuvier, 1822

Synonyms—*Aphelotherium* Gervais, 1848
Leptadapis Gervais, 1852
Palaeolemur Delfortrie, 1873

Adapis parisiensis Blainville, 1841[1]
Adapis magnus Filhol, 1874
Adapis rutimeyeri Stehlin, 1912
Adapis priscus Stehlin, 1916
Adapis sciureus Stehlin, 1916

PROTOADAPIS Lemoine, 1891
Synonyms—*Plesiadapis :* Lemoine, 1878 (in part)
Protadapis : Stehlin, 1912
Megatarsius Weigelt, 1933
Europolemur Weigelt, 1933
Protoadapis curvicuspidens[2] Lemoine, 1878
Synonym—*Protadapis recticuspidens :* Stehlin 1912 (in part)
Protoadapis angustidens (Filhol, 1888)
Synonyms—*Adapis angustidens* Filhol, 1888
Protadapis brachyrhynchus Stehlin, 1912
Protoadapis klatti (Weigelt, 1933)
Synonyms—*Europolemur klatti* Weigelt, 1933
Megatarsius abeli Weigelt, 1933

CAENOPITHECUS Rütimeyer, 1862
Caenopithecus lemuroides Rütimeyer, 1862

PRONYCTICEBUS Grandidier, 1904
Pronycticebus gaudryi Grandidier, 1904

ANCHOMOMYS Stehlin, 1916
Synonym—*Caenopithecus :* Rütimeyer, 1891
Anchomomys pygmaeus (Rütimeyer, 1891)
Anchomomys gaillardi Stehlin, 1916
Anchomomys quercyi Stehlin, 1916
Anchomomys latidens Teilhard, 1916

GESNEROPITHEX Hürzeler, 1946
Gesneropithex peyeri Hürzeler, 1946

Family MICROSYOPIDAE new sense, McKenna (1960)

ALSATICOPITHECUS Hürzeler, 1947
Alsaticopithecus leemanni Hürzeler, 1947

?Primates *incertae sedis*

AMPHILEMUR Heller, 1935
Amphilemur eocaenicus Heller, 1935

---

[1] For numerous synonyms of the various species of *Adapis*, see Stehlin (1912, 1916).
[2] Here designated as the type species of *Protoadapis*.

VII. CONCLUSIONS

The occurrence of a new omomyid prosimian genus, *Cantius*, from the English Sparnacian is reported on and its distinctions from the Middle Eocene genus *Protoadapis* outlined. Assignment of this form to the Omomyidae reinforces the extension of the range of this family into the Old World suggested by a few previously described forms. Although additional resemblances to North American notharctids are noted for *Protoadapis*, it is referred to the Adapidae on the basis of its greater similarities with *Caenopithecus* and *Pronycticebus*. Preliminary evidence suggests that Notharctidae and Adapidae, as defined by Gazin (1958) may not actually be distinguishable, but solution of this problem requires additional comparative study.

Certain loris-like features of the genus *Pronycticebus* are pointed out. Just possibly, these can be interpreted as indicating the differentiation of the lorisiform prosimians from the general stock of the Adapidae (*s.l.*). A high degree of dental similarity between an undoubted lorisoid prosimian, *Progalago*, of the early Miocene of Kenya, and the late Eocene European primate *Anchomomys* is stressed. These findings are in contrast to the widespread opinion that no close relationship of early Cenozoic with Recent prosimian families can be demonstrated, but is in line with the vertical taxonomic association of necrolemurines and tarsiines proposed by Simons (1961). However, zoogeographical and morphological considerations alone are sufficient to indicate that it would be unwise to regard any such relationships direct ancestor-descendant lineages.

A number of species previously regarded as *incertae sedis* are here re-assigned or removed from the order and the taxonomy of European Eocene Primates revised.

VIII. ACKNOWLEDGEMENTS

I should like to thank Dr. K. P. Oakley of the British Museum (Natural History), Dr. J.-P. Lehman of the National Museum of Natural History, Paris, and Drs. H.-W. Matthes and G. Krumbiegel of the Geological and Paleontological Institute of the Martin Luther University of Halle/Wittenburg for the opportunity to study and report on Eocene Primates in their respective collections. Thanks are also due to Dr. G. L. Jepsen of Princeton University, Sir Wilfrid Le Gros Clark, and to many others with whom this subject has been discussed. Figures were prepared by Miss Christine Court of Oxford University and Mrs. Margaret E. Freeman of New Haven, and early completion of the work facilitated by a grant from the Wenner-Gren Foundation for Anthropological Research.

IX. REFERENCES

Abel, O. 1931. *Die Stellung des Menschen im Rahmen der Wirbeltiere.* 398 pp. Jena.

Barnett, C. H. & Napier, J. R. 1953. The rotatory mobility of the fibula in eutherian mammals. *J. Anat. Lond.*, **87** : 11–21.

Chow, Min-chen. 1961. A New Tarsioid Primate from the Lushi Eocene, Honan. *Vertebrata Palasiatica*, Peking, **5** : 1–5, 3 figs.

Clark, W. E. Le Gros. 1934. On the skull structure of *Pronycticebus gaudryi. Proc. Zool. Soc. Lond.*, **1934** : 19–27, 3 figs.

—— 1956. A Miocene lemuroid skull from East Africa. *Fossil Mammals of Africa*, **9**, 6 pp. 1 pl. British Museum (Nat. Hist.), London.

CLARK, W. E. LE GROS & THOMAS, D. P. 1952. The Miocene Lemuroids of East Africa. *Fossil Mammals of Africa*, **5**, 20 pp., 3 pls. British Museum (Nat. Hist.), London.

COOPER, C. FORSTER. 1932. On some mammalian remains from the Lower Eocene of the London Clay. *Ann. Mag. Nat. Hist.*, London (10) **9** : 458–467, pls. 11–12.

FILHOL, H. 1888. Description d'une nouvelle espéce d'*Adapis*. *Bull. Soc. philom. Paris*, **7**, 12 : 10–12.

FORSYTH MAJOR, C. I. 1901. On some characters of the skull in the lemurs and monkeys *Proc. Zool. Soc. Lond.*, **1901** : 129–153, pls. 11–13.

GAZIN, C. L. 1958. A review of the Middle and Upper Eocene Primates of North America. *Smithson Misc. Coll.*, Washington, **126** : 1–112, pls. 1–14.

GRANDIDIER, G. 1904. Un noveau Lemurien fossile de France, le *Pronycticebus Gaudryi*. *Bull. Mus. Hist. nat. Paris*, **10** : 9–13, 3 figs.

—— 1905. Les lemuriens disparus. *Nouv. Arch. Mus. Hist. nat. Paris* (4) **7** : 1–42.

GREGORY, W. K. 1920. On the structure and relations of *Notharctus*, an American Eocene primate. *Mem. Amer. Mus. Nat. Hist.*, New York (n.s.) **3** : 49–243, pls. 23–59.

—— 1922. *The origin and evolution of the human dentition.* xviii + 548 pp., 14 pls. Baltimore.

GRANGER, W. & GREGORY, W. K. 1917. A revision of the Eocene Primates of the genus *Notharctus*. *Bull. Amer. Mus. Nat. Hist.*, New York, **37** : 841–859, pls. 103–107.

HELLER, F. 1930. Die Säugetier fauna der mitteleozänen Braunkohle des Geiseltals bei Halle. *Jb. hallesch. Verb. Erf. mitteldtsch. Bodensch.*, Halle (n.f.) **9** : 13–41, pls. 1–5.

—— 1935. *Amphilemur eocaenicus* n. g. et n. sp., ein primitiver Primate aus dem Mitteleozan des Geiseltales bei Halle a. S. *Nova Acta Leop. Carol.*, Halle a. S. (n.s.) **2** : 293–300.

HILL, W. C. O. 1953. *Primates. Comparative Anatomy and Taxonomy. I. Strepsirhini.* xxiv + 798 pp., 34 pls. Edinburgh.

—— 1955. *Primates. Comparative Anatomy and Taxonomy. II. Haplorhini : Tarsioidea.* 347 pp., 14 pls. Edinburgh.

HÜRZELER, J. 1946. *Gesneropithex Peyeri* nov. gen. nov. spec. von Gosgen (Solothurn). *Ecl. geol. Helv.*, Lausanne, **39**, 2 : 354–361, 4 figs.

—— 1947. *Alsaticopithecus Leemanni* nov. gen. nov. spec., ein neuer Primate aus dem unteren Lutetien von Buchsweiler im Unterelsass. *Ecl. geol. Helv.*, Lausanne, **40** : 343–356, 12 figs.

—— 1948. Zur Stammesgeschichte der Necrolemuriden. *Abh. schweiz. paläont. Ges.*, Zurich, **66** : 1–46, 41 figs.

—— 1950. Über die europäischen Apatemyiden. *Ecl. geol. Helv.*, Lausanne, **42**, 2 : 485.

JEPSEN, G. L. 1934. A revision of the American Apatemyidae and the description of a new genus, *Sinclairella*, from the White River Oligocene of South Dakota. *Proc. Amer. Phil. Soc.*, Philadelphia, **74** : 287–305, pls. 1–3.

LEMOINE, V. 1878. Communication sur les ossements fossiles des terrains tertiares inférieurs des environs de Reims. *Bull. Soc. Hist. nat. Reims*, **1878** : 90–113, pls. 1–5.

—— 1891. Étude d'ensemble sur les dents des mammifères fossiles des environs de Reims. *Bull. Soc. geol. Fr.*, Paris (3) **19** : 263–290, pls. 10, 11.

LEMOINE, V. & AUMONIER, M. 1880. Terrains tertiaires des environs de Reims. *Ass. Franc. Avanc. Sci.*, Paris, **9** : 605–619, pl. 5.

MATTHES, H. W. 1957. Die mitteleozane Saugerfauna des Geiseltales and ihre verwandschaftlichen Beziehungen. *Wiss. Z. Univ. Halle, Math. Nat.*, **7** : 37–62, 22 figs.

MCKENNA, M. C. 1960. Fossil mammalia from the early Wasatchian Four Mile fauna, Eocene of northwest Colorado. *Bull. Dep. Geol. Univ. Calif.*, Berkeley, **37** : 1–130, 64 figs.

OSBORN, H. F. 1891. A review of the Cernaysian Mammalia. *Proc. Acad. Nat. Sci. Philad.*, **1890** : 51–62, 6 figs.

PIVETEAU, J. 1957. Primates, paléontologie humain. *Traité de Paléont.*, Paris, **7** : 1–675.

RUSSELL, D. E. 1960. Le crane de *Plesiadapis*. *Bull. Soc. géol. Fr.*, Paris, **7** : 312–314, pl. 18.

RÜTIMEYER, L. 1862. Eocäne Säugethiere aus dem Gebiete des schweizerischen Jura. *Denkschr. schweiz. Ges. Naturw.*, Zurich, **19** : 1–248, pls. 1–6.

—— 1891. Die Eocäne Säugethier-welt von Egerkingen. *Abh. schweiz. paläont. Ges.*, Zurich, **18** : 1–153, pls. 1–8.

SIMONS, E. L. 1961. Notes on Eocene Tarsioids and a revision of some Necrolemurinae. *Bull. Brit. Mus.* (*Nat. Hist.*) *Geol.*, London, **5** : 43–69, pls. 12–14.

—— 1961*a*. The dentition of *Ourayia* :—its bearing on relationships of omomyid prosimians. Postilla, Yale Peabody Mus., New Haven, Conn., **54** : 1–20, 3 figs.

SIMONS, E. L. & RUSSELL, D. E. 1960. Notes on the cranial anatomy of *Necrolemur*. *Breviora Mus. Comp. Zool. Harv.*, Cambridge, Mass., **127** : 1–14, 3 figs.

SIMPSON, G. G. 1940. Studies on the earliest primates. *Bull. Amer. Mus. Nat. Hist.*, New York, **77** : 185–212, 8 figs.

—— 1945. The principles of classification and a classification of mammals. *Bull. Amer. Mus. Nat. Hist.*, New York, **85** : 1–350.

—— 1955. The Phenacolemuridae, new family of early primates. *Bull. Amer. Mus. Nat. Hist.*, New York, **105** : 415–441, pls. 30–35.

STEHLIN, H. G. 1912. Die Saugetiere des schweizerischen Eocaens. *Abh. schweiz. paläont. Ges.*, Zurich, **38** : 1165–1298, figs, 244–288.

—— 1916. Die Saugetiere des schweizerischen Eocaens. *Abh. schweiz. paläont. Ges.*, Zurich, **41** : 1299–1552, pls. 21–22.

STEHLIN, H. G. & SCHAUB, S. 1951. Die trigonodontie der simplicidentaten nager. *Abh. schweiz paläont. Ges.*, Zurich, 67 : 1–385, 620 figs.

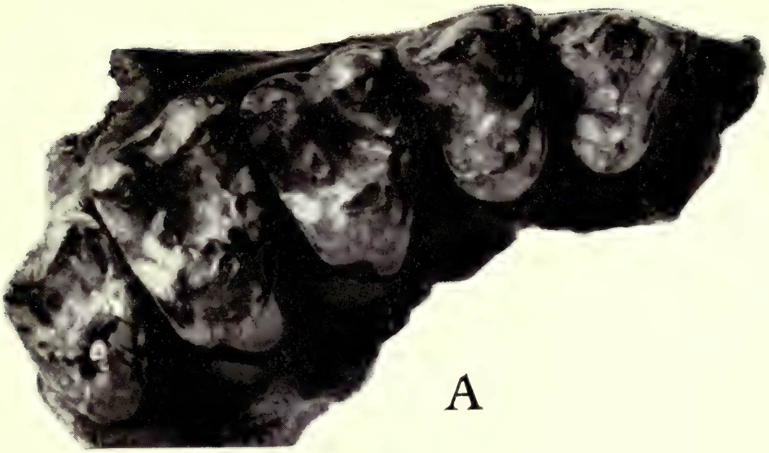
TEILHARD DE CHARDIN, P. 1921. Les mammifères de l'Eocene inférieur Français et leurs gisements. *Ann. Paléont.*, Paris, **10** : 171–176 ; **11** : 9–116, 42 figs.

WEIGELT, J. 1933. Neue Primaten aus der mitteleozanen (oberluteitischen) Braunkohle des Geiseltals. *Nova Acta Leop. Carol.*, Halle (n.f.) **1** : 97–156, pls. 1–11.

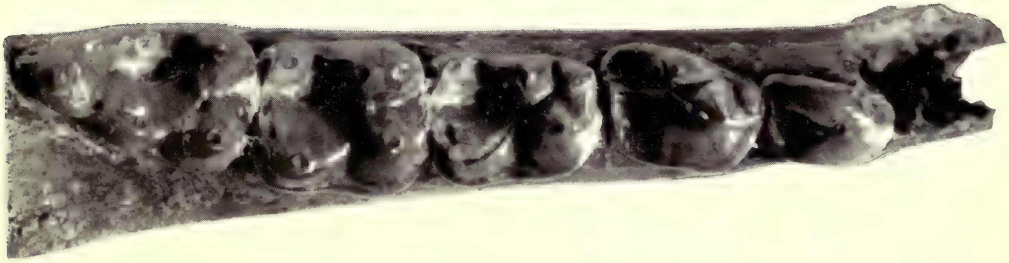
PLATE 1

Cantius eppsi (Cooper)

A. Right maxilla, B.M.N.H., M 15145, with P^3–M^2. B. Right mandible, B.M.N.H., M 13773 (Type), with P_3–M_3. ×6·0 approx.



A



B

PLATE 2

Protoadapis klatti (Weigelt)

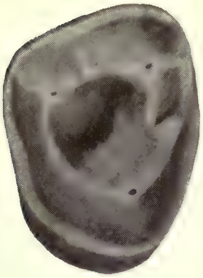
Anterior dentition, G.P.I.H. 4258. × 7·3 approx.

PLATE 3

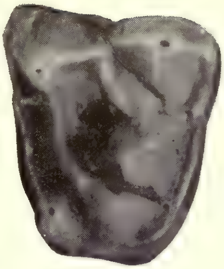
Protoadapis klatti (Weigelt)

Specimens of *Protoadapis* at Halle. A. Right M^3, G.P.I.H. 7325 ; B. Right M^1, G.P.I.H. 4292 ; C. Right M^2, cf. *Protoadapis*, G.P.I.H. 4238 ; D. Left M^3, G.P.I.H. 4292 ; E. Left M^{2-3}, Left P_4–M_3, G.P.I.H. 4310. All ×8·0 approx.

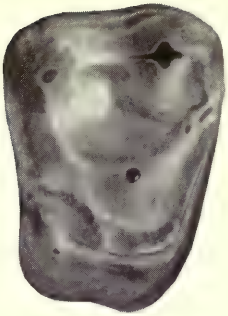
(Photographs slightly retouched.)



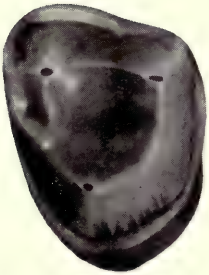
A



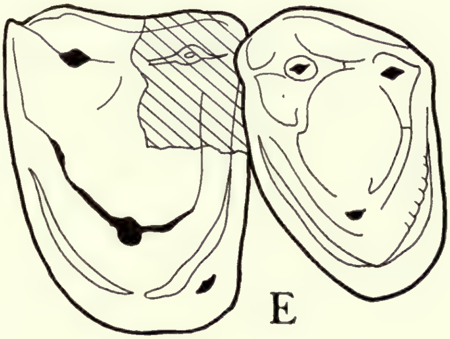
B



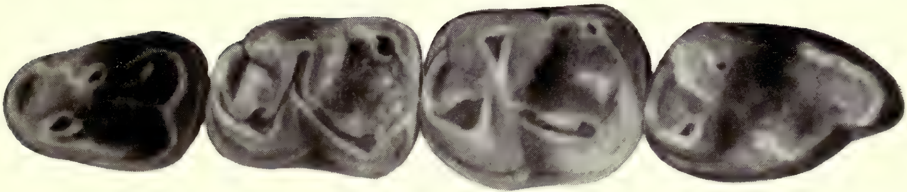
C



D



E



F

PRINTED IN GREAT BRITAIN BY
ADLARD AND SON, LIMITED
BARTHOLOMEW PRESS DORKING

THE BRACHIOPOD GENUS *CYCLOTHYRIS*

BRITISH MUSEUM
4 JUN 1962
NATURAL HISTORY

E. F. OWEN

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 7 No. 2
LONDON: 1962

THE BRACHIOPOD GENUS *CYCLOTHYRIS*

BY

ELLIS FREDERIC OWEN

4 JUN 62

Pp. 37–63 ; *Pls.* 4, 5 ; 10 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 7 No. 2
LONDON : 1962

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series, corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

This paper is Vol. 7 No. 2 of the Geological (Palaeontological) series.

© Trustees of the British Museum, 1962

PRINTED BY ORDER OF THE TRUSTEES OF
THE BRITISH MUSEUM

Issued May, 1962 *Price Fourteen Shillings*

THE BRACHIOPOD GENUS *CYCLOTHYRIS*

By ELLIS FREDERIC OWEN

SYNOPSIS

A revision of M'Coy's genus *Cyclothyris* from the Upper Aptian is made and serial sections of the type-species presented for the first time. In addition eight other species of *Cyclothyris* are described, two of these are new species. The subfamily Cyclothyrinae of Makridin is emended and discussed. A comparison is made between *Cyclothyris* from the Lower Greensand and the Upper Chalk genus *Cretirhynchia*. A new generic name is proposed for five Lower Cretaceous Rhynchonellidae.

INTRODUCTION

THE name *Cyclothyris* was first used by M'Coy (1844 : 103) to indicate a group of brachiopods which he called " . . . those curious species in which the deltidium completely surrounds the foramen ". No geological age was mentioned nor was any species named. M'Coy did, however, figure a specimen (p. 150, fig. 29) which is probably lost.

From the beak characters of Mesozoic and Palaeozoic Rhynchonellidae it seems likely that M'Coy was referring to an early Cretaceous genus and, from the arrangement of the costae, shell outline, growth-marks and interarea as seen in his fig. 29, it is probable that M'Coy had selected a specimen of Aptian age.

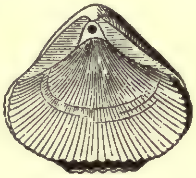


FIG. 1. Copy of M'Coy's (1844) original illustration of fig. 29, p. 150.

Previously, J. de C. Sowerby (1825 : 165, pl. 502, fig. 1) had described and figured a rhynchonellid from the Upper Aptian, Sponge Gravel of Faringdon, Berkshire under the name *Terebratula lata*. He subsequently changed this specific name to *T. latissima* in the index to the *Mineral Conchology* published in 1829, having realized that his father J. Sowerby (1815 : 227) had already used the name *T. lata* for a brachiopod from the Drift of Lowestoft, Suffolk.

The outline, arrangement of costae and growth-lines of J. de C. Sowerby's figured specimen of *Terebratula latissima* (pl. 502, fig. 1) agree with the figure of M'Coy's genus *Cyclothyris*. This similarity was certainly noted by Davidson (1855 : 93) who included *Cyclothyris* in his synonymy of Fischer's genus *Rhynchonella* and quoted *C. latissima* in brackets after the generic name, probably as a typical species of *Cyclothyris*.

Buckman (1906 : 326) was the first to designate *T. latissima* J. de C. Sowerby as the type species of *Cyclothyris* and subsequent authors have followed Buckman. The genus was not further investigated nor adequately defined until Hertlein & Grant (1944 : 61) published a full synonymy in their work on Caenozoic Brachiopoda from western North America.

Stratigraphically the genus ranges from the Upper Aptian to the Upper Cenomanian and was probably developed from such a middle European form as *Lepidorhynchia* which Burri (1956 : 689) described from the Neocomian, Lower Barremian, of Switzerland. *Cyclothyris* appears to have been confined chiefly to the European continent, although a notable exception to this is *C. americana* described and figured by Cooper (1955 : 3, pl. 1) from the Aptian of Arizona. Examples of this species have not yet been examined by the writer but to judge from the figure on Cooper's pl. 1 it may well belong to this genus. Other species referred to *Cyclothyris* by Hertlein & Grant (1944 : 63) are probably not referable to the genus, but careful examination including the use of serial sections is necessary before any conclusions can be drawn. Another species from the American continent referred to this genus is *Cyclothyris* ? *subtrigonalis* Imlay from the Lower Neocomian of Mexico. This is shown in serial section (Imlay, 1937 : 571) to have a persistent septum in the brachial

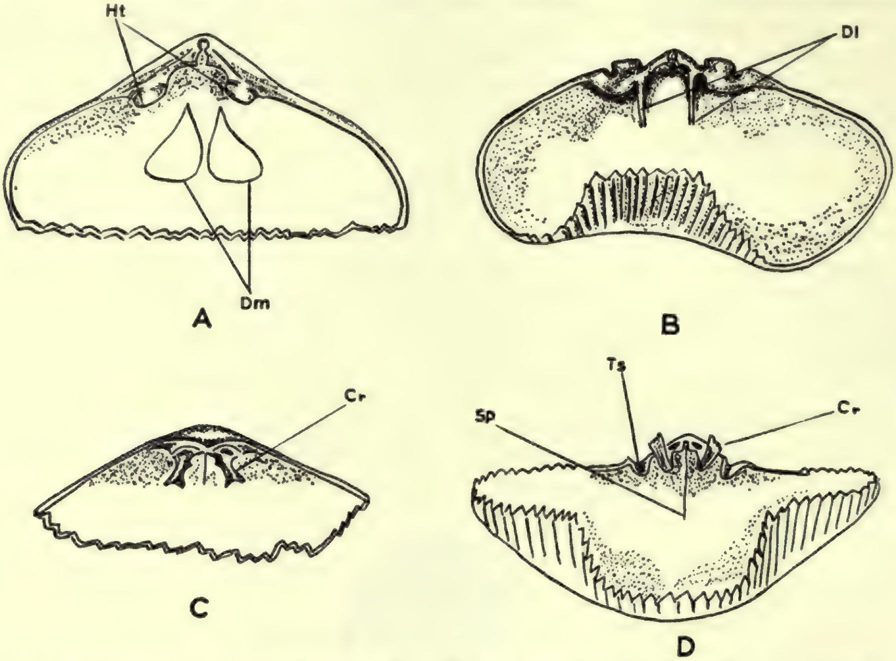


FIG. 2. Four drawings illustrating some of the internal characters of *Cyclothyris*. A. Pedicle valve showing subquadrate hinge-teeth (*Ht*) and large pear-shaped diductor muscle-scars (*Dm*). B. Subparallel dental lameleae in pedicle valve (*Dl*). C. Brachial valve showing ventral surface of the crura (*Cr*). D. Brachial valve showing the dorsal concave surface of the crura (*Cr*) and deep crenulated dental sockets (*Ts*) and short septum (*Sp*).

valve and a large septalium, both characters which do not appear in serial sections of the type species *C. latissima* (J. de C. Sowerby).

In the English Aptian the genus is represented by at least four species namely, *C. latissima*, *C. depressa* (J. de C. Sowerby), *C. antidichotoma* (Buvignier) and *C. lepida* sp. n., but there may be others not yet investigated. The rhynchonelloid species "*R.*" *nuciformis* described from the Upper Aptian of Faringdon by J. de C. Sowerby (1825 : 166), and often erroneously referred to *Cyclothyris*, is probably related to a species described by the writer (Owen, 1960 : 253) as *Lamellaerhynchia larwoodi* from the Upper Aptian of Upware, Cambridge.

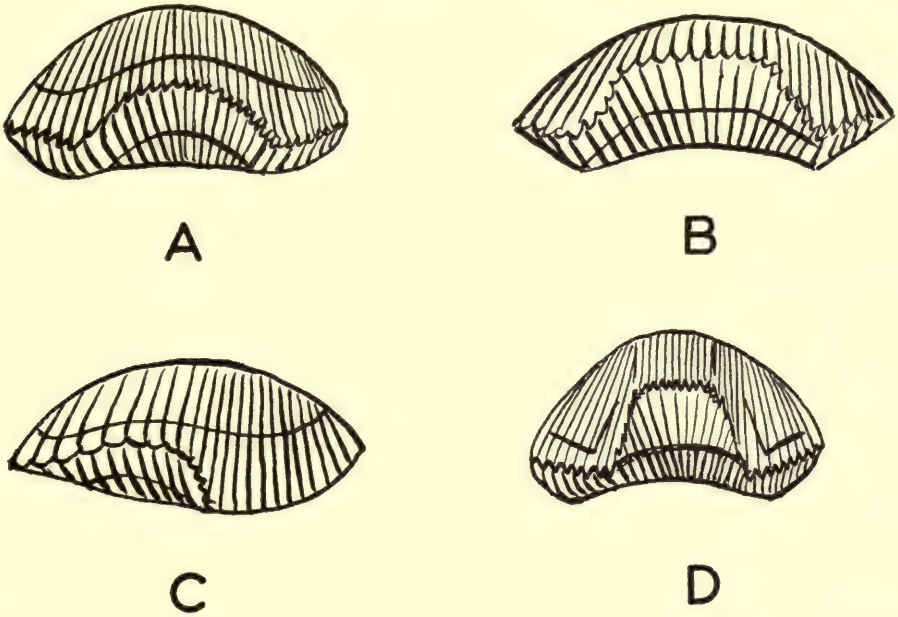


FIG. 3. Diagram illustrating different types of anterior commissure found in *Cyclothyris*. A. Broadly arcuate. B. Trapezoidal. C. Asymmetrical. D. High arcuate.

Some of these Upper Aptian species are recognizable as passage forms in the Lower Albian deposits at Leighton Buzzard, Bedfordshire. Middlemiss (1959 : 138) regards the Shenley Limestone fauna as essentially of an Albian-Cenomanian type. While possibly true of the terebratuloid fauna it is certainly not of the rhynchonelloids. With the possible exception of two species the fauna is distinctly Albian, having close affinities with Upper Aptian faunas at Brickhill and Upware in this country and Lower Albian faunas at Grandpré, Haute-Savoie and Haute-Saône, France.

Two Lower Albian species of *Cyclothyris* are described here from the *Leymeriella tardefurcata* Zone of the Shenley Limestone of Leighton Buzzard, Bedfordshire. One is the widely quoted *C. antidichotoma* (Buvignier), which also occurs in the Upper Aptian, and *C. levis* sp. n.

By far the commonest Cenomanian species of *Cyclothyris* is *C. difformis* (Valenciennes *in* Lamarck) which ranges from the Lower to Middle Cenomanian. It has been recorded from Wiltshire, Devon and Dorset in England and from Normandy in France, Tournai in Belgium, and Essen in North Germany. Examples of this species with its many varieties are to be found in the general collections of the British Museum (Natural History).

Apart from *C. difformis*, other Cenomanian species here described include *C. scaldisensis* (d'Archiac) from the Tourtia of Belgium, and *C. schloenbachi* (Davidson), a common fossil in the Lower Cenomanian of Somerset and Devon.

The generic name *Burrirhynchia* is proposed for "*Rhynchonella*" *leightonensis* Walker from the Lower Albian, *L. tardefurcata* Zone of Shenley Hill, Leighton Buzzard, Bedfordshire. This genus is also represented in the Upper Aptian, *P. nutfieldensis* Zone, of Upware, Cambridge and Brickhill, Buckinghamshire by the species "*R.*" *cantabrigensis* Davidson.

An emended description of "*R.*" *leightonensis* together with serial sections were published by the writer (Owen, 1956 : 166, 167) and these may be compared with serial sections of *Burrirhynchia cantabrigensis* (Davidson) figured here as Text-fig. 10.

TERMINOLOGY

The terms used in the systematic descriptions here are according to Thomson (1927), Muir-Wood (1934) and Muir-Wood & Cooper (1960).

Cyclothyrid. As applied to the deltidial plates was proposed by the writer (Owen, 1956 : 165) to replace the term "*auriculate*" which was used by Buckman (1918 : 18) to describe the encirclement of the foramen by the deltidial plates.

Sulcus. The term *sinus* has often been used by authors to describe the median sulcation of a valve. Muir-Wood & Cooper (1960 : 8) pointed out that the term for this condition should be *sulcus*. Their definition was in connection with productoids, but the term is equally applicable to the rhynchonelloids and is quoted as "Sulcus.—A major depression in either valve usually median in position, which helps channel the outgoing stream in feeding. A median fold is usually opposite a median sulcus in the productoids."

The term *sulcus*, therefore, as defined by Muir-Wood & Cooper is used throughout the following systematic descriptions.

In the same publication Muir-Wood & Cooper (1960 : 14) redefined the following terms :

Capillae. Fine radial, elevated lines (with more than 25 in 10 mm.).

Costellae. Radial lines coarser than capillae (about 15–25 in 10 mm.).

In the following systematic descriptions the measurement of 10 mm. is taken to indicate a position 10 mm. wide at a distance 10 mm. anterior to the umbo on the brachial valve. These terms have been used as above in the descriptions of *C. antidichotoma*, *C. lepida* sp. n. and *C. levis* sp. n.

Dimensions of *Cyclothyris* specimens are given in millimetres but are defined generally as :

Small, measuring up to 15 mm. long, 20 mm. wide.

Medium, 16–28 mm. long, 21–38 mm. wide.

Large, 29–35 mm. long, 39–45 mm. wide.

SYSTEMATIC DESCRIPTIONS

Superfamily RHYNCHONELLACEA Schuchert, 1896

Family RHYNCHONELLIDAE Gray, 1848

Rzhonitskaya (1959), in an attempt to reclassify the rhynchonelloids, cited the subfamily Cyclothyrinae which was proposed by Makridin (1955) for certain rhynchonelloid genera ranging from the Trias to the Cretaceous. Makridin's definition quoted by Rzhonitskaya is translated by Mrs. G. A. Cooper, Washington, U.S.A. as :

" Ribbed or plicate rhynchonellids without a septalium ; septa may be developed or be absent, hinge-plate divided."

This very broad definition included such genera as *Stolmorhynchia* Buckman, 1914 and *Lacunosella* Wisniewska, 1932 which, unlike most of the other genera included, are known to possess falcifer crura and are quite distinct from those genera bearing radulifer crura.

The following emended definition of Makridin's subfamily Cyclothyrinae is therefore proposed :

Costate, costellate, capillate or plicate rhynchonelloids without a septalium ; septum developed or absent, hinge-plates divided, crura radulifer, foramen hypothyrid.

This would include the following genera :

Cyclothyris M'Coy, 1844.
Cretirhynchia Pettitt, 1950.
Sulcirhynchia Burri, 1953.
Lamellaerhynchia Burri, 1953.
Plicarostrum Burri, 1953.
Lepidorhynchia Burri, 1956.
Burrirhynchia nov.

RANGE. Cretaceous.

Subfamily CYCLOTHYRINAE Makridin, 1955 emended

Genus ***CYCLOTHYRIS*** M'Coy, 1844

1844 *Cyclothyris* M'Coy, p. 103, 150, fig. 29.
1852 *Cyclothyris* Davidson, p. 93.
1877 *Cyclothyris* Dall, p. 24.
1906 *Cyclothyris* Buckman, p. 18.
1913 *Cyclothyris* Schuchert *in* Zittel, p. 398.
1918 *Cyclothyris* Buckman, pl. 14, fig. 1*a*.

TYPE-SPECIES (by subsequent designation, Buckman, 1906). *Terebratula latissima* J. de C. Sowerby.

EMENDED DIAGNOSIS. Medium to large biconvex rhynchonellidae, oval to subtriangular in outline. Shell multicostate, costae sharp, coarse to fine, subangular to rounded. Growth-lines lamellar to step-like. Anterior commissure uniplicate. Beak-ridges usually distinct, interarea well defined. Foramen medium to large, circular. Deltidial plates conjunct, cyclothyrid.

Internal characters. Umbonal cavities oval in cross-section. Denticulae well developed. Teeth large, deeply inserted. Dental lamellae strong, subparallel. Hinge-plates broad, slightly arched in transverse section, divided terminally. Crura anteriorly concave.

DESCRIPTION. *Cyclothyris* comprises a very variable group of medium to large rhynchonellidae. With the exception of perhaps one or two species, the outline is distinctly transversely oval. A fold and sulcus develop late and there is usually considerable lateral and anterior thickening of the margins in the gerontic stage. The ornament consists chiefly of strong costae with marked growth-lines sometimes becoming lamellar. The type and position on the valves of the growth-lines is regarded as a specific character and can be linked with type of costation when grouping the species. The members of the *latissima* group, for instance, have numerous subangular or rounded radiating costae with fairly distinct growth-lines at about one-third the distance from the umbo, and approximately three to five at about two-thirds the distance from the umbo. They tend to be closer together or more lamellar and less prominent at the anterior margin. Bifurcation of the costae in adult forms is rare.

In some species, notably *C. antidichotoma* (Buvignier), the ornament shows considerable deviation from the typical. Davidson (1851, pl. 14) in the species *Capillirhynchia wrighti* (Davidson) from the Inferior Oolite, and Ager (1958 : 69) in *Furcirhynchia furcata* Buckman from the Lias illustrated a similar kind of ornament. In the genus *Cyclothyris* this type of ornament is regarded as a specific character.

Marked uniplication of the anterior margin is a strong feature but some species show a tendency to produce an asymmetrical commissure. These aberrant forms are noticeable throughout the generic range and particularly in the Cenomanian species *C. difformis*.

Some species, for instance *C. scaldisensis* (d'Archiac), are characterized by their large circular foramen. This is a common feature of the *latissima* group.

Internal characters

Pedicle valve. The umbonal cavity is roughly oval in cross-section, a pedicle collar being developed within the first 4 mm. The cyclothyrid deltidium is seen in transverse section as two outwardly curving plates, one on either side of the foramen. The crenulated hinge-teeth are thick, quadrate and deeply inserted, expanding dorsally. The diductor muscle-scars are large and triangular. The adductor muscle-scars are too faint for adequate description.

Brachial valve. No cardinal process is developed. The hinge-plates are slender and gently arched ventrally. Inner and outer socket-ridges are well defined. The median septum is short and does not support the hinge-plates. Radulifer crura originate from the distal parts of the hinge-plates and curve ventrally. Each terminates in a Y-shaped fork which may be slightly deflected dorsally or remains almost horizontal to the sides of the valve.

DISCUSSION. The chief distinguishing characters of *Cyclothyris*, apart from its general outline, are the extensive interarea, absence of bifurcation and intercalation of costae in adult forms, large circular foramen and incipient fold in the brachial valve. The arched and divided or forked hinge-plates, as seen in transverse section, distinguish it from other Cretaceous rhynchonellid genera. It is readily distinguished from *Orbirhynchia* (Pettitt, 1954) in possessing radulifer crura.

The stratigraphical zones quoted for species of *Cyclothyris* from the Lower Greensand are according to Casey (1961).

Cyclothyris latissima (J. de C. Sowerby)

(Pl. 4, figs. 7, 8 ; Text-fig. 4)

1825 *Terebratula lata* J. de C. Sowerby (*non T. lata* J. Sowerby), p. 165, pl. 502, fig. 1.
1829 *Terebratula latissima* J. de C. Sowerby, Index.
1852 *Rhynchonella latissima* (J. de C. Sowerby) : Davidson, p. 82, pl. 11, figs. 15–22.
1918 *Cyclothyris latissima* (J. de C. Sowerby) : Buckman, p. 14, pl. 14, fig. 1*a*.
1950 *Cyclothyris latissima* (J. de C. Sowerby) : Pettitt, pl. 1, figs. 14, 15.
1956 *Cyclothyris latissima* (J. de C. Sowerby) : Owen, pl. 3, fig. 6.

EMENDED DIAGNOSIS. Medium sized *Cyclothyris* approximately 21 mm. long, 24 mm. wide and 13 mm. thick. Transversely oval to subtriangular in outline, lenticular in anterior contour. Brachial valve convex, with broad, flat almost imperceptible median fold. Pedicle valve less convex, with broad shallow sulcus. Anterior commissure broadly arcuate. Umbo short, thick, slightly incurved. Foramen large. Deltidial plates well exposed. Each valve ornamented by about 60 rounded or subangular costellae (23 per 10 mm.) with approximately 13 on the fold and a corresponding number in the sulcus.

LECTOTYPE. In the original description of the species J. de C. Sowerby (1825 : 165) quotes three localities, Faringdon, Sidmouth, and Devizes Canal. The species is represented in the Sowerby Collection, British Museum (Natural History) by three specimens from the above localities. Of these, the specimen from Faringdon was selected and figured as lectotype of the species by Pettitt (1950, pl. 1). It is registered in the British Museum (Natural History) collections as B.61499. Of the two remaining syntypes, one is recognizable as a young *C. difformis* (Valenciennes *in* Lamarck) from the Cenomanian of Sidmouth, Devon, while the other is crushed and too badly damaged for identification.

DESCRIPTION. Although *C. latissima* does not seem to show the same range of variation as other species of *Cyclothyris*, a marked variant occurs at Faringdon, Berkshire and at Brickhill, Buckinghamshire and reaches dimensions considerably larger than the typical form, measuring approximately 25 mm. long, 34 mm. wide and 18 mm. thick. The dimensions of the lectotype are 21 mm. long, 28 mm. wide and 12 mm. thick. A fine series of specimens illustrating the above variant are to be found in the collections of the Sedgwick Museum, Cambridge numbered SM. B.25682–B.25708.

The outline of the shell of *C. latissima* remains oval to subtriangular with a broad flat fold on the brachial valve. The ornament consists of approximately 60 costellae on each valve, which are characteristically subangular or rounded and interrupted by step-like or fairly steep concentric growth-lines at about one-third the distance from the umbo and again at about two-thirds the distance from the umbo. Growth-lines at the anterior margin tend to be more numerous, usually about 3 to 5 and are lamellar.

Internal structure. As for genus. Text-fig. 4.

Cyclothyris latissima can be distinguished from other Aptian species of *Cyclothyris* by its more acutely triangular outline, more extensive interarea, less marked anterior fold and more prominent growth-lines. It differs from *C. depressa* (J. de C. Sowerby) in its less produced beak, larger dimensions, less angular costellae and more arcuate anterior commissure. It is less convex than other *Cyclothyris* species with the exception of *C. scaldisensis* (d'Archiac) from the Tourtia of Belgium which it resembles, but can be distinguished from this species by its smaller dimensions, more prominent growth-lines and less well-developed interarea and beak-ridges.

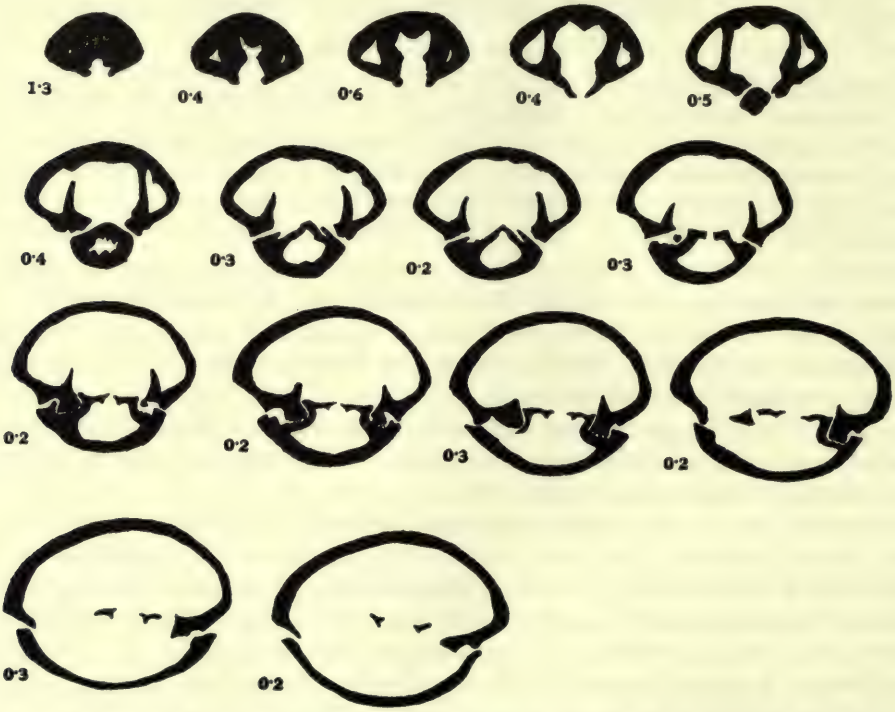


FIG. 4. A series of fifteen transverse serial sections through the umbonal part of a specimen of *Cyclothyris latissima* (J. de C. Sowerby) from the type locality, Faringdon, Berkshire. BM. BB.5482. × 2.

DISTRIBUTION. Apart from the type locality at Faringdon, Berkshire, where it occurs in the *Tropaeum subarcticum* subzone of the *Parahoplites nutfieldensis* Zone, *C. latissima* has also been found in the *P. nutfieldensis* Zone at Upware, Cambridge and from the junction of the Hythe and Sandgate Beds on the foreshore just west of Folkestone Harbour, Kent.

Cyclothyris antidichotoma (Buvignier)

(Pl. 4, figs. 3–6 ; Text-figs. 5, 6)

1842 *Terebratula antidichotoma* Buvignier, p. 533, pl. 4 fig. 8.
1847 *Rhynchonella antidichotoma* (Buvignier) d'Orbigny, p. 31, pl. 500, figs. 1–5.
1847 *Rhynchonella antidichotoma* (Buvignier) : Pictet & Roux, p. 534, pl. 50, figs. 5*a–g*.
1872 *Rhynchonella antidichotoma* (Buvignier) : Pictet, p. 41, pl. 199, figs. 13–17*b*.
1874 *Terebratula antidichotoma* Buvignier : Davidson, p. 65, pl. 8, figs. 19–21.
1903 *Rhynchonella lineolata* var. *mirabilis* Walker, p. 261, pl. 18, figs. 7*a–c*.

EMENDED DIAGNOSIS. Medium to large biconvex *Cyclothyris* approximately 31 mm. long, 36 mm. wide and 15 mm. thick. Transversely oval to subcircular in outline. Brachial valve with broad, faintly developed median fold. Pedicle valve with wide, shallow sulcus, anteriorly developed. Anterior commissure broadly arcuate to trapezoidal. Umbo massive to sharp, slightly produced. Foramen large. Deltidial plates well exposed. Beak-ridges distinct, interarea extensive. Each valve ornamented with between 15 and 30 fine rounded costellae posteriorly and a few strong angular costae anteriorly.

TYPE SPECIMEN. The original specimen figured by Buvignier (1842, pl. 4, fig. 8) cannot be traced and is presumed lost. It is not proposed to erect a neotype of this species until more material from the type locality has been examined. The only available specimen said to be from the area of the type locality examined by the writer is in the d'Orbigny Collection, Muséum Nationale d'Histoire Naturelle, Paris and is registered in the d'Orbigny catalogue as 6014. This specimen, stated to be from the Albian of Saulce, Ardennes, does not resemble Buvignier's figured specimen in general outline although the ornament is similar. Instead it resembles one of the more robust forms commonly found in England at Brickhill and Upware and regarded as an extreme variant. D'Orbigny (1847, pl. 500) figured two specimens both of which resemble the one figured by Buvignier (1842, pl. 4, fig. 8). Neither of these specimens is in the d'Orbigny Collection and their whereabouts cannot be ascertained.

DESCRIPTION. Buvignier's figure shows a large *Cyclothyris* measuring approximately 32 mm. long and 42 mm. wide, with a sharp beak, large foramen and ornament of fine costellae and strong costae which are the main distinguishing features. Specimens possessing similar features have been examined by the writer from Upware, Cambridgeshire, Brickhill, Buckinghamshire and Potton and Leighton Buzzard, Bedfordshire. In addition collections of specimens also bearing these features from Albian localities in France and Switzerland have been studied in the Muséum d'Histoire Naturelle, Geneva.

It is probable that the original specimen described by Buvignier came from the Gault of Grandpré, although specimens of other species from this locality are usually preserved as internal casts in phosphatized sandy clay. Buvignier's specimen, however, has a well-preserved shell and may have come from the beds below the phosphate workings which are known to be of Upper Aptian age.

In England, the Upper Aptian forms occurring at Brickhill and Upware differ from Buvignier's figured specimen in their more circular general outline and more convex valves, although variants approaching the typical form have been found. The Lower Albian forms from Leighton Buzzard, while agreeing in general outline and proportions with Buvignier's figure, have a less acute apical angle, less produced beak and smaller interarea and are much nearer a form which occurs at Goudinière, Grand St. Bernard and at Mont Saxonet, Savoie, France. This form is represented in the Davidson Collection, British Museum (Natural History) by three specimens from Goudinière registered as BB.41485–87. Another specimen showing a marked resemblance to the Leighton Buzzard form comes from the Albian of Vergys, Upper Savoie and is registered as BM. B.35284.

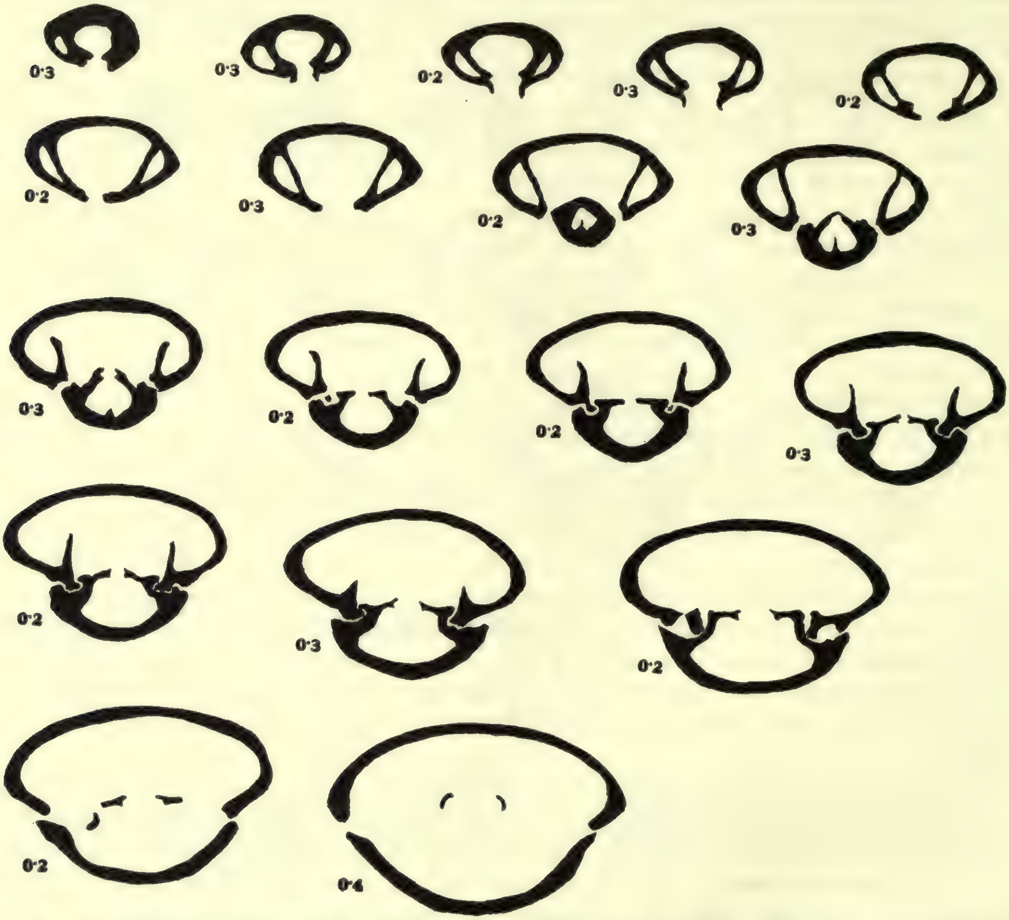


FIG. 5. Eighteen transverse serial sections through the umbonal part of *Cyclothyris antidichotoma* (Buvignier) from the Upper Aptian, Upware, Cambridge. BM. B.25753. × 2.

Young forms of this species were thought to belong to a new variety by Walker (1903 : 261) who described them as *Rhynchonella lineolata* var. *mirabilis*. They are usually more triangular in outline than the adult forms, with marked anterior sulcation of both valves. The large marginal costae are less numerous at this stage and the median fold in the brachial valve is not developed. Examples of this juvenile stage were figured by Pictet & Roux (1847, pl. 50) and by Pictet (1872, pl. 919) as *R. antidichotoma* (Buvignier).

The ornament of fine costellae and coarse costae running into one another is characteristic of the species but, as already stated, authors have described a similar feature on species in the Jurassic, and less notably, on Upper Cretaceous species such as *Cretirhynchia octoplicata* (J. Sowerby) as figured by Davidson (1852, pl. 10, figs. 1–11).

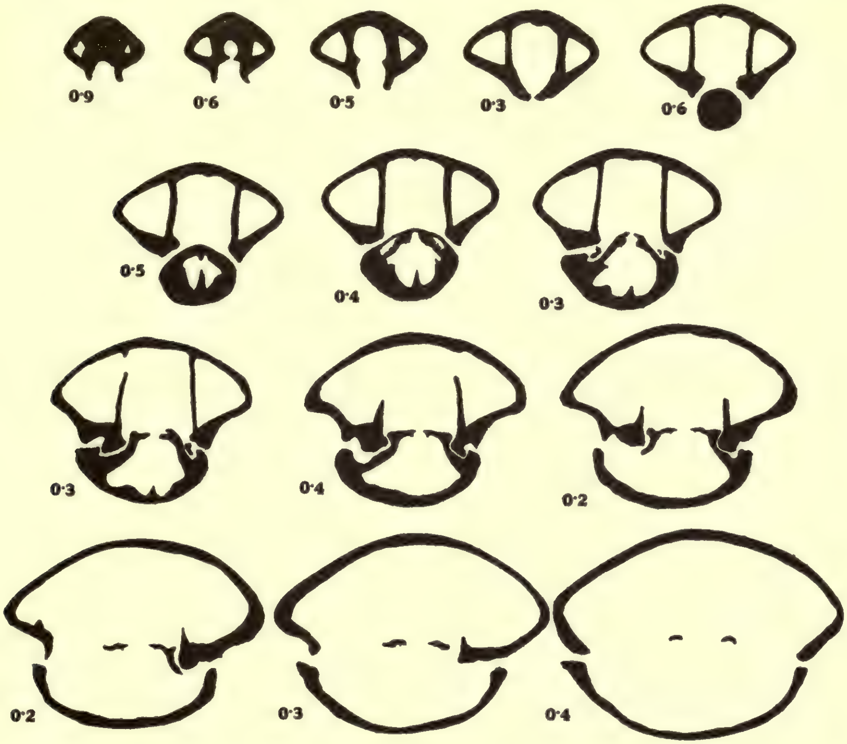


FIG. 6. Fourteen transverse serial sections through the umbonal part of *Cyclothyris antidichotoma* (Buvignier) from the Lower Albian, Shenley Hill, Leighton Buzzard, Bedfordshire. BM. BB.17561. × 2.

Although there may be sufficient grounds both morphologically and stratigraphically for separating the Upper Aptian forms from those in the Lower Albian of this country, the writer proposes to leave this extremely well-known species as it is at present interpreted until more material from Grandpré, or at least from the French Ardennes, is available and the limits of variation are possible to define.

DISTRIBUTION. *C. antidichotoma* as at present interpreted is a common fossil in the Upper Aptian, *P. nutfieldensis* Zone, at Upware, Cambridge and Brickhill, Buckinghamshire and occurs, though not commonly, in the Lower Albian, *Leymeriella tardefurcata* Zone at Leighton Buzzard, Bedfordshire. It has also been collected from the Albian of Mont Saxonet and Goudinière and from the Ardennes, France.

Cyclothyris depressa (J. de C. Sowerby)

(Pl. 4, fig. 11)

1825 *Terebratula depressa* J. de C. Sowerby, p. 165, pl. 502, fig. 3.
1852 *Rhynchonella depressa* (J. de C. Sowerby) Davidson, p. 89, pl. 11, figs. 28–32.

EMENDED DIAGNOSIS. Small *Cyclothyris* about 9 mm. long, 11 mm. wide and 8 mm. thick. Elongate-triangular in outline. Brachial valve convex with moderately well-developed median fold. Pedicle valve less convex with shallow sulcus. Anterior commissure uniplicate with trapezoidal linguiform extension. Beak suberect, apical angle acute. Foramen large. Deltidial plates well exposed. Shell ornamented by about 25–28 sharp, angular, radiating costae originating from the umbones, with 6 on fold and 7–8 in sulcus.

LECTOTYPE. In the original description of the species J. de C. Sowerby (1825) figured two specimens as fig. 3 on his pl. 502. Of these the larger of the two specimens is shown in dorsal and ventral views. This specimen is here selected as lectotype of the species. It is in the Sowerby Collection, British Museum (Natural History) No. B.61468, together with the second figured specimen (B.61469) and three other syntypes (B.61470–72) which are also referable to *C. depressa.*

DESCRIPTION. Apart from its small dimensions, the distinctive characters of this species are those of the beak, which is slightly produced, sharp and suberect. The large circular foramen shows the cyclothyrid deltidial plates to advantage. The pedicle valve has a marked trapezoidal linguiform extension. The sharp, angular costae show no signs of bifurcation or intercalation. They are interrupted only by a faint growth-line which appears at about two-thirds the distance from the umbo to anterior margin.

Internal structure. As for genus.

REMARKS. *C. depressa* has been grouped with *C. schloenbachi* (Davidson) since the two species have much in common. Their general outline and profile is roughly the same with a well-defined fold and sulcus. The linguiform extension is trapezoidal in shape. Both species are relatively small and seem to show the same extremes of variation with fine and coarse costation. *C. depressa*, however, is distinguished from *C. schloenbachi* by its more acutely triangular outline, slightly produced beak and shallower sulcus in the pedicle valve and well-developed fold on the brachial valve. It differs from *C. latissima* in its general triangular outline, angular costation, produced beak, smaller dimensions and trapezoidal linguiform extension.

DISTRIBUTION. *C. depressa* is commonly found in association with *C. latissima* in the Upper Aptian (*P. nutfieldensis* Zone) of Faringdon, Berkshire and also at the same horizon at Brickhill, Buckinghamshire.

Cyclothyris difformis (Valenciennes *in* Lamarck)

(Pl. 5, figs. 1–7 ; Text-figs. 7, 8)

1819 *Terebratula difformis* Valenciennes *in* Lamarck, p. 255, fig. indicated *Encycl. Meth.*, 1789, pl. 242, fig. 5.
1821 *Terebratula dimidiata* J. Sowerby, p. 138, pl. 277, fig. 5.
1822 *Terebratula gallina* Brongniart, p. 84, pl. 9, fig. 2.
1828 *Terebratula deformis* Lamarck : Defrance, p. 160, pl. 5, fig. 3.
1847 *Rhynchonella compressa* (Lamarck) : d'Orbigny, p. 35, pl. 497, figs. 1–5.
1850 *Terebratula difformis* Lamarck : Davidson, p. 433, pl. 15, fig. 48.
1852 *Terebratula compressa* Lamarck : Davidson, p. 80, pl. 11, figs. 4, 5.
1885 *Terebratula difformis* Lamarck : Quenstedt, p. 696, pl. 54, fig. 2.
1900 *Rhynchonella difformis* (Lamarck) Jukes-Browne, p. 65, figs. 41, 42.
1918 *Terebratula difformis* Valenciennes *in* Lamarck : Clerc & Favre, pl. 15, fig. 84.

EMENDED DIAGNOSIS. Medium-sized *Cyclothyris* approximately 23 mm. long, 31 mm. wide and 17 mm. thick. Shell biconvex, fold low, indistinct, oval to subtriangular in outline. Anterior commissure with well-marked uniplication. Umbo short, massive, slightly incurved. Foramen fairly large. Deltidial plates conjunct, well exposed. Beak-ridges distinct. Interarea extensive. About 40–45 costae on either valve (14 per 10 mm.) with 9 on fold and 10–11 in sulcus.

LECTOTYPE. Owing to Lamarck's blindness the brachiopods in his " Animaux sans Vertèbres " (vol. 6, 1819) were described by his pupil A. Valenciennes from specimens in Lamarck's own collection. In the description of *Terebratula difformis* (p. 255) Valenciennes indicated a specimen illustrated in *Encyclopédie Méthodique* (1789, pl. 242, fig. 5) quoting the localities " near Le Mans, and also at Cap la Hève, near Le Havre " both Cenomanian localities. No type specimen was named or indicated and the whereabouts of the figured specimen is not known.

Davidson (1850 : 433) in a description of Lamarck's species states that he borrowed the ten specimens used by Valenciennes in his original description and figured one of them as *T. difformis* (pl. 15, fig. 48). This would have served as lectotype of the species had the specimen not been subsequently lost or mislaid. A further specimen figured by Clerc & Favre (1918, pl. 15, figs. 84*a–d*) has therefore been selected as lectotype of the species. This specimen is one of eight to be found under the name *Terebratula difformis* in the Lamarck Collection at the Muséum d'Histoire Naturelle, Geneva and is registered as No. 48 in the Lamarck catalogue. From the mode of preservation and adhering matrix it was almost certainly collected from the Lower Cenomanian of the Normandy coast. The other seven specimens are probably of Jurassic age. The dimensions of the lectotype are : 23 mm. long, 31 mm. wide and 17 mm. thick.

DESCRIPTION. *C. difformis* is an extremely variable species ranging in outline from subcircular to transversely oval to subtriangular. The ornament usually consists of about 45 coarse to relatively fine costae originating from the umbo of each valve and becoming more elevated towards the anterolateral margins. These costae are usually interrupted by one or two step-like growth-lines situated at about one-half to two-thirds the distance from the umbo to the anterior margin.

The umbo varies from short to massive to slightly produced. An extensive interarea with distinct beak-ridges is seen throughout the range of variation. The median fold on the brachial valve remains indistinct while the broad, shallow sulcus in the pedicle valve is late in development. The linguiform extension varies from broadly arcuate to trapezoidal but asymmetry of the anterior commissure is a notable character.

Variants worthy of special note occur at Wilmington, south Devon and at Cap la Hève, Normandy. One of the Wilmington varieties departs from the typical in having more convex valves, shorter umbo, smaller foramen and more acutely arched anterior commissure. The variety usually found on the Normandy coast, on the other hand, has a slightly produced beak, less convex valves and commonly exhibits an asymmetrical anterior commissure.

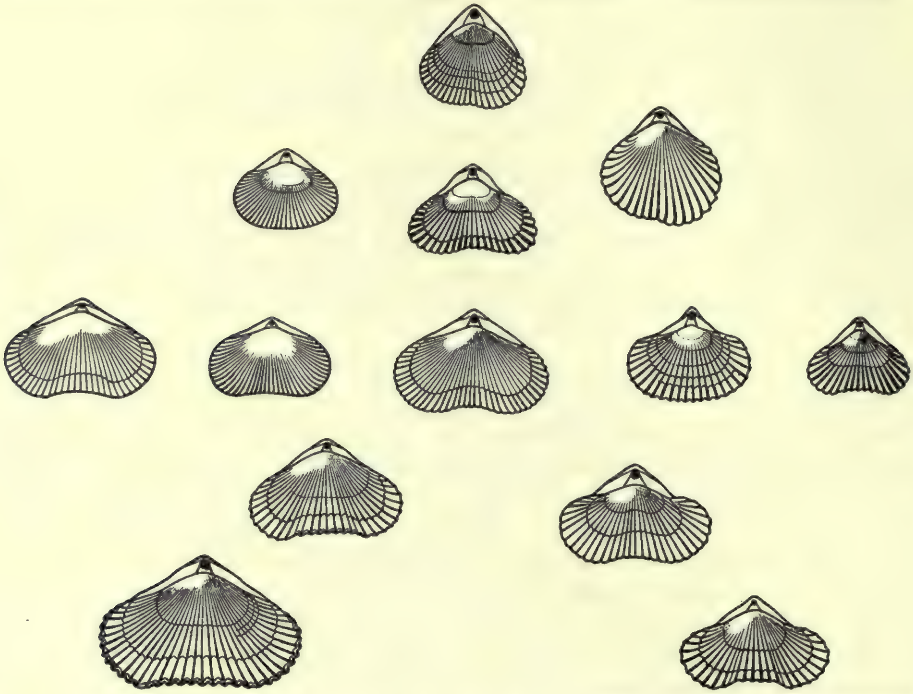


FIG. 7. Diagram illustrating thirteen variants of *Cyclothyris difformis* (Valenciennes *in* Lamarck) from Wiltshire, south Devonshire, and Normandy.

Another notable variant occurs in the Lower Cenomanian, Tourtia, Belgium. Six well-preserved specimens in the British Museum (Natural History) are numbered BB.41475–80. The same variety occurs in the Lower Cenomanian deposits of Essen, North Germany and is represented in the same museum by a single specimen (BB. 41473).

The specimen figured and described as *Terebratula dimidiata* by J. Sowerby (1821 : 138, pl. 277, fig. 5) from Halldown near Chudleigh, south-east Devon, is a large, almost sphaeroidal rhynchonellid with coarse costae, sharp, produced beak and asymmetrical anterior commissure. This is either an extreme variant of *C. difformis* or a pathological form.

A form somewhat resembling the outline of Sowerby's *T. dimidiata* but with finer costae, is figured by d'Orbigny (1847, pl. 498, figs. 6–9) from the Charentes as *Rhynchonella difformis*. Some authors have followed d'Orbigny's interpretation of Lamarck's species and Mlle G. Fage (1935 : 433, pl. 11), in a description of some Upper Cretaceous rhynchonellids from the Charentes, illustrated an evolutionary development from *R. difformis* d'Orbigny to a variety *R. globata* Fage. Her figured specimen of *R. difformis* is stated to have been collected from the Coniacian.

A specimen figured by J. de C. Sowerby (1836, pl. 18, fig. 2) as *T. dilatata* was stated in the explanation of the plates to have been collected from Blackdown, south Dorset.

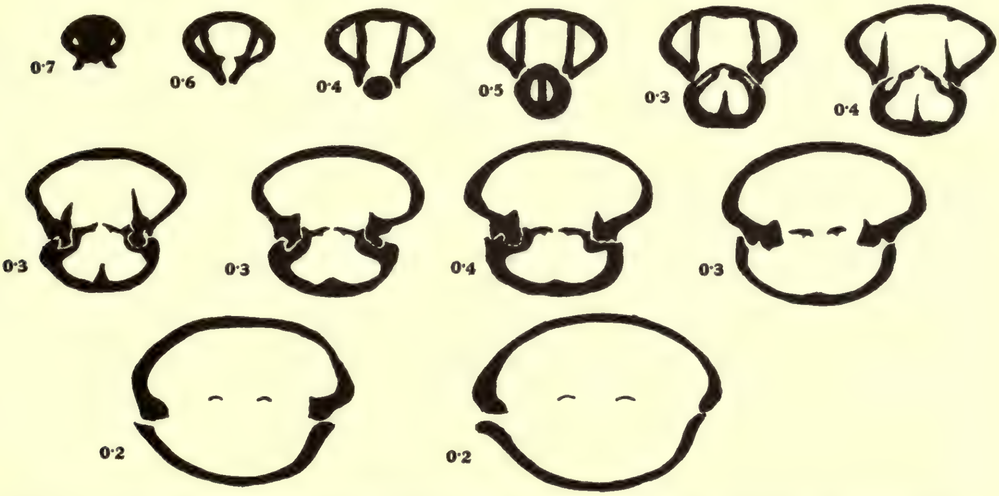


FIG. 8. A series of twelve transverse serial sections through the umbonal part of *Cyclothyris difformis* (Valenciennes *in* Lamarck) from the lower Cenomanian, Cap la Hève, near Le Havre, Normandy. BM. B.35224. × 2.

This figure shows a remarkable similarity to a specimen figured by Schloenbach (1867, pl. 23, fig. 2) as *C. difformis* from the Lower Cenomanian of Essen, Germany.

DISTRIBUTION. *C. difformis* ranges from the Lower to Middle Cenomanian of the west of England, Normandy and North Germany. In the type area of the Normandy coast it occurs in the remanié bed at the base of the Cenomanian, is abundant in the Lower Cenomanian and is less common, but still well represented in the Middle Cenomanian.

In England the species is almost unrepresented in the Middle Cenomanian though rare examples have been found in the Middle Cenomanian basement beds of west Dorset. It is abundant, however, in the Lower Cenomanian, occurring in Wiltshire (Warminster Greensand) and the Devon coast, as well as in the Isle of Wight. A well-marked variant is the commonest brachiopod in the sandy Lower Cenomanian of Wilmington, south Devon. It is said to occur in the *dispar* Zone at Punfield Cove, south Dorset but specimens of this species are more likely to have been collected from the bottom Cenomanian beds. Its occurrence below this level is uncertain.

Cyclothyris compressa (Valenciennes *in* Lamarck)

(Pl. 5, fig. 8)

1819 *Terebratula compressa* Valenciennes *in* Lamarck, p. 256, No. 54.
1850 *Terebratula compressa* Lamarck : Davidson, p. 455, pl. 15, fig. 54.
1918 *Terebratula compressa* Valenciennes *in* Lamarck : Clerc & Favre, pl. 19, figs. 117, 119.

EMENDED DIAGNOSIS. *Cyclothyris*, about 28 mm. long, 32 mm. wide and 14 mm. thick. Distinctly subtriangular in general outline ; brachial valve convex with faint median fold. Pedicle valve posteriorly convex with broad, shallow median sulcus. Both valves ornamented by about 40 strong, acutely angular, radiating costae, (8 per 10 mm.) with 8 on fold and a corresponding number in sulcus. Concentric growth-lines very faint. Beak short, slender, slightly incurved. Beak-ridges distinct, interarea small. Deltidial plates triangular, foramen small.

LECTOTYPE. The specimen here selected as lectotype of the species is one of four syntypes in the Lamarck Collection at the Muséum d'Histoire Naturelle, Geneva and is numbered in the Lamarck Catalogue as No. 54. The specimen was figured by Davidson (1850, pl. 15, fig. 54) and by Clerc & Favre (1918, pl. 19, fig. 117). It was collected from the Upper Cenomanian of Coulaines near Le Mans in the Sarthe, south-west of the Paris basin. The dimensions of the lectotype are : 29 mm. long, 35 mm. wide and 14 mm. thick.

DESCRIPTION. *C. compressa* is one of the most distinctive species of *Cyclothyris*. It is characterized by its acutely subtriangular outline and strong angular costae. It can be distinguished by its low, faintly developed median fold, trapezoidal linguiform extension, and marginal thickening of the valves. It is probable that this species is a direct development of *C. difformis*. A specimen from the Tourtia of Belgium, showing characters of both species is in the British Museum (Natural History) numbered BM. B.1889. Another specimen figured by Davidson (1852, pl. 11, figs. 4, 5) as *C. compressa* and figured here on Pl. 5, fig. 8 as *C. difformis* shows the general outline of *C. difformis* with the anterior and lateral contours and sharp angular costae of *C. compressa* but without the marginal thickening of the valves.

DISTRIBUTION. The species, originally described from Coulaines near Le Mans in the Sarthe, France is confined to the sandy Cenomanian of the south-west Paris basin. The typical form is characteristic of the Upper Cenomanian, Sables du Perche, where it is the only rhynchonellid present. Related but not identical forms occur in the beds above (Marnes à *Ostrea biauriculata*) and below (Sables et Grès du Mans).

Varieties, stated to belong to this species, were described by Cayeux (1949) from Le Havre but were not accompanied by any adequate description or illustration, nor were any type-specimens indicated.

Cyclothyris schloenbachi (Davidson)

(Pl. 4, figs. 12, 13)

1852 *Rhynchonella depressa* vars. A and B, Davidson, p. 92, pl. 12, figs. 28–30.
1874 *Rhynchonella schloenbachi* Davidson, p. 59.

EMENDED DIAGNOSIS. Small *Cyclothyris* about 11 mm. long, 15 mm. wide and 13 mm thick. Shell outline oval, brachial valve convex, slightly inflated, with well-defined median fold. Pedicle valve less convex with shallow sulcus broadening anteriorly. Foramen medium sized to small. Beak-ridges distinct, interarea fairly long. Ornament varying from fine to coarse costae.

LECTOTYPE. *C. schloenbachi* was first described by Davidson (1874 : 59) who included three specimens which he had previously described and figured (1852 : 92, pl. 12, figs. 28–30) as varieties A and B of *Rhynchonella depressa* (J. de C. Sowerby), an Upper Aptian species. Two of these specimens (figs. 28, 29) were collected from the Cenomanian of Chardstock, Somerset, BM. B.8215, and the third (fig. 30) from the Cenomanian of Shaftesbury, Wiltshire. Of these syntypes, the specimen from Shaftesbury (BM. B.8216), figured by Davidson (1852, pl. 12, fig. 30) is here selected as lectotype of the species.

DESCRIPTION. *Cyclothyris schloenbachi* is a common fossil is the Lower Cenomanian beds of south Devon, Somerset, south Wiltshire, and Dorset. As can be seen from Davidson's original figures (1852, pl. 12, figs. 28–30) the ornament varies from fine, subangular to strong, coarse costae. Davidson himself (1874 : 59) noted this variation and stated that intermediate forms were commonly found with the extreme forms.

The median fold is better developed or more distinct on specimens with finer costae and is often replaced in the coarser costate forms by a slight sulcation of the brachial valve.

Bifurcation of the costae is a fairly common feature of the young coarsely costate forms. Both variants occur with intermediate forms in the same beds at Chardstock in Somerset, Beer Head, Devon, and Pinhay Cliff, Dorset.

Because of its comparatively small dimensions *C. schloenbachi* cannot easily be confused with other known *Cyclothyris* species. It is distinguished from the somewhat similar *C. depressa* by its oval outline, less produced beak, smaller foramen and better developed or deeper sulcus in the pedicle valve.

DISTRIBUTION. In England, *C. schloenbachi* appears to be confined to the Lower Cenomanian beds of south Devon, Dorset, Somerset and Wiltshire. A slightly larger form of the same species occurs in the Lower Cenomanian beds of Vivautier in the department of Orne, France and is represented in the Davidson Collection, British Museum (Natural History) by fifteen specimens numbered B.11917. These specimens show variations identical with those of the English forms.

Cyclothyris lepida sp. n.

(Pl. 4, fig. 10)

DIAGNOSIS. *Cyclothyris* about 22 mm. long, 32 mm. wide and 16 mm. thick. Shell biconvex, transversely oval in outline. Brachial valve with poorly developed median fold. Pedicle valve with broad shallow sulcus. Both valves ornamented by about 60–65 fine rounded costellae (21 per 10 mm.) with 20 on the fold and about 22 in the sulcus. Anterior contour lenticular. Linguiform extension trapezoidal, moderately developed. Beak prominent with large foramen.

HOLOTYPE. SM. B.25683 from the Upper Aptian, Brickhill, Buckinghamshire in the collections of the Sedgwick Museum, Cambridge.

Dimensions of holotype. 26 mm. long, 33 mm. wide and 16 mm. thick.

PARATYPES. Twenty-two specimens from the type locality in the Sedgwick Museum SM. B.25682, B.25684–87, B.25689–702, B.25706–08. Also 40 specimens from the same locality and horizon in the British Museum (Natural History), B.25546, B.25547, B.25549.

DESCRIPTION. *C. lepida* is a medium-sized *Cyclothyris* with a characteristic ornament of fine radiating costellae originating from the umbones of each valve. The absence of any prominent growth-lines gives the species a neat appearance. The beak is strong and slightly incurved. An extensive interarea is bounded by distinct beak-ridges. The foramen is large and the deltidial plates well exposed.

Internal characters. As for genus.

REMARKS. This species can be distinguished from others of *Cyclothyris* mainly by its distinctly oval outline, fine costellae, regular anterior commissure, moderately developed but well-marked median fold on the brachial valve, trapezoidal linguiform extension and absence of marked growth-lines. It occurs with *C. antidichotoma* (Buvignier) at Brickhill but its ornament shows none of the characteristics of this species. It is probably the species referred to by authors as *Rhynchonella lata* d'Orbigny (1847 : 21) from the Neocomian of France.

Because if its regular outline, well-marked median fold and absence of prominent growth-lines, *C. lepida* is grouped with *C. depressa* and *C. schloenbachi*.

DISTRIBUTION. *C. lepida* appears to be confined to the Upper Aptian of Brickhill, Buckinghamshire.

Cyclothyris levis sp. n.

(Pl. 4, fig. 9)

DIAGNOSIS. *Cyclothyris* about 20 mm. long, 24 mm. wide and 12 mm. thick. Shell biconvex, distinctly subtriangular in outline. No median fold developed on brachial valve. Shallow, broad sulcus developed anteriorly in pedicle valve. Both valves covered by about 100 very fine capillae (48 per 10 mm.). Beak short, massive, foramen small. Beak-ridges distinct. Interarea small. Deltidial plates not well exposed.

HOLOTYPE. BB.41493 in British Museum (Natural History) from the Lower Albian (*L. tardefurcata* Zone) of the Shenley Limestone, Leighton Buzzard, Bedfordshire. Dimensions of holotype are : 22 mm. long, 27 mm. wide and 14 mm. thick.

PARATYPES. Sixty-one specimens in British Museum (Natural History) registered Nos. B.26541, B.26542, B.26595. .

DESCRIPTION. In general outline this species resembles *C. latissima* but has a much more inflated brachial valve. A broad, shallow sulcus develops late in the pedicle valve giving rise to a low broadly arcuate anterior commissure. The short, slightly incurved beak is sharp and massive with a small circular foramen. Distinct beak-ridges define a small interarea. Faint concentric growth-lines are seen on both valves and appear more distinct towards the anterolateral margins.

Internal characters. As for genus.

REMARKS. *C. levis* is distinguished from other *Cyclothyris* species by its extremely fine, rounded capillae, short massive beak, absence of median fold in the brachial valve and poorly developed sulcus in the pedicle valve. It can be distinguished from *C. lepida* sp. n. mainly by its general subtriangular outline, fine capillae, absence of median fold, shorter more massive beak, less extensive interarea, poorly exposed deltidial plates and broad arcuate anterior commissure. Although resembling *C. latissima* in general outline it can be distinguished from this species by its less extensive interarea, less produced beak, finer ornament of capillae, less marked growth-lines and broader arcuate anterior commissure.

DISTRIBUTION. *Cyclothyris levis* is confined to the Lower Albian and is a common fossil in the limestone lenticles (*L. tardefurcata* Zone) at Leighton Buzzard, Bedfordshire.

Cyclothyris scaldisensis (d'Archiac)

(Pl. 4 fig. 1)

1846 *Terebratula scaldisensis* d'Archiac, p. 330, pl. 21, fig. 11.

EMENDED DIAGNOSIS. *Cyclothyris* about 24 mm. long, 32 mm. wide and 16 mm. thick. Shell biconvex, oval to subtriangular in outline, brachial valve with broad incipient median fold. Broad flattened median sulcus in pedicle valve. Umbo short, massive, slightly incurved. Foramen large, circular. Deltidial plates well exposed. Costae fine, rounded, numbering about 68 on each valve (12 per 10 mm.) with 15–18 on the fold and a corresponding number in the sulcus.

HOLOTYPE. The specimen used by d'Archiac in his description of the species was stated to have been collected from the Tourtia of Belgium. It is not certain whether this specimen is still extant and enquiries are still being made. Several well-preserved specimens from the Tourtia of Belgium are to be found in the Davidson Collection and in the general collections of the British Museum (Natural History). Two good examples of this species are from Tournai and are registered B.1889, BB.41492. Another specimen, larger than the dimensions given for the typical form, is figured here on Pl. 4, fig. 1.

DESCRIPTION. *C. scaldisensis* is medium sized, characteristically oval to broadly subtriangular in outline. The brachial valve is convex and slightly inflated posteriorly with a very faintly developed median fold. The pedicle valve is convex in the umbonal region but develops a shallow sulcus which broadens anteriorly. The linguiform extension is moderately developed giving rise to a low broad, arcuate anterior commissure. Both valves are ornamented by about 65–68 fairly fine, rounded costae radiating from the umbones. Faint lamellar growth-lines are seen at about half and again at two-thirds the distance from the beak to the anterior margin. They tend to become more prominent anteriorly. The short umbo is massive with a large circular foramen and well-exposed deltidial plates. The beak-ridges are distinct and define a faintly concave extensive interarea.

This is probably the least variable of all species of *Cyclothyris*. Its characteristically fine, rounded costae and faint concentric growth-lines make it easily distinguishable from *C. difformis*, with which it is often associated. It differs from *C. latissima*, from which it was most probably developed, by its less prominent growth-lines, longer or more extensive interarea and less incurved beak.

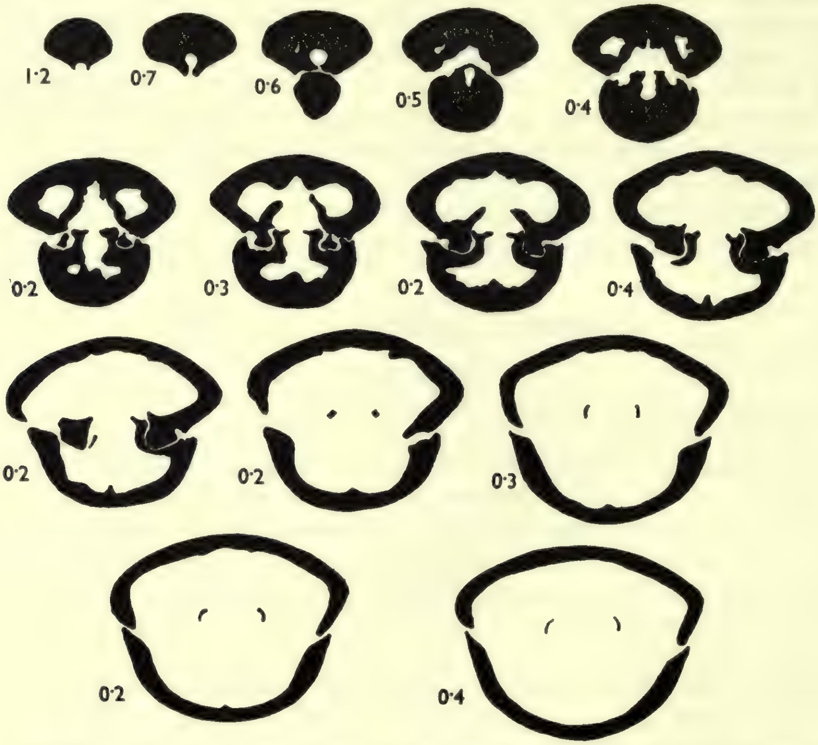


FIG. 9. Fourteen transverse serial sections through the umbonal part of *Cretirhynchia norvicensis* Pettitt from the Upper Chalk (*mucronata* Zone), Mousehold Pit, Norwich. BM. B.25079. ×2.

DISTRIBUTION. Apart from the area of its original description in the Lower Cenomanian, Tourtia, of Belgium, the species is recorded from the Lower Cenomanian of Honfleur, Cap la Hève and Fécamp, Normandy and from a similar horizon in the Munster basin at Essen, Germany. It also occurs, though not commonly, in the Lower Cenomanian beds of Wiltshire, and the south Devon coast.

Genus ***BURRIRHYNCHIA*** nov.

DIAGNOSIS. Small to medium biconvex rhynchonellidae. Usually elongate-triangular in general outline. Umbo massive, suberect; beak-ridges rounded.

Foramen small, circular, hypothyrid. Deltidial plates disjunct, cyclothyrid. Anterior commissure with broad trapezoidal linguiform extension Faint fold on brachial valve. Hinge plates narrow, ventrally arched. Median septum strong, persistent. Ornament of fine, rounded costellae (more than 50 on each valve).

TYPE SPECIES. " *Rhynchonella* " *leightonensis* Walker, 1903.

HOLOTYPE. From Lower Albian (*L. tardefurcata* Zone), Shenley Hill, Leighton Buzzard, Bedfordshire, No. GSM. 51279 in the Geological Survey Museum.

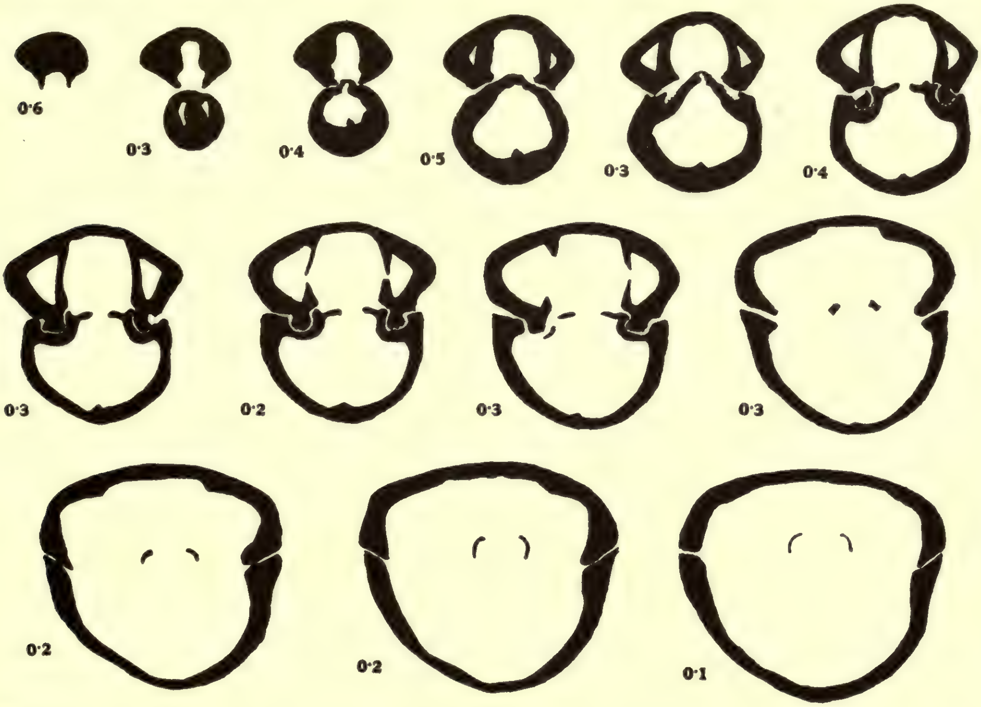


FIG. 10. A series of thirteen serial sections through the umbonal part of *Burrirhynchia cantabrigensis* (Davidson) from the Upper Aptian of Upware, Cambridge. B.M. B.25749. × 2.

REMARKS. The genus differs from *Cyclothyris* in its more elongate-triangular outline, strong persistent median septum, small foramen, rounded beak-ridges, and narrow hinge-plates which are not terminally divided. In transverse outline it resembles *Sulcirhynchia* Burri (1953) from the Swiss Neocomian, from which it may have been developed. It can be distinguished from this genus, however, by its stronger, more persistent, median septum, narrower, less acutely ventrally deflected hinge-plates, shorter, less deeply inserted hinge-teeth and more clearly defined inner and outer socket-ridges.

Burrirhynchia almost certainly gave rise to *Cretirhynchia* Pettitt, 1950, from the Upper Chalk but is distinguished from it by its subparallel dental lamellae, disjunct deltidial plates, poorly defined interarea and absence of bifurcation of costellae and thicker, less clearly defined hinge-plates.

RANGE. Upper Aptian to Lower Albian.

SPECIES ASSIGNED. "*R.*" *leightonensis* Walker, "*R.*" *cantabrigensis* Davidson, "*R.*" *gibbsiana* (J. de C. Sowerby), "*R.*" *bertheloti* d'Orbigny. "*R.*" *tripartita* Pictet.

MATERIAL AND LOCALITIES. One hundred and sixty specimens of *B. leightonensis* (Walker) from the Lower Albian (*L. tardefurcata* Zone), Shenley Hill, Leighton Buzzard, Bedfordshire (B.26524–28, B.26595), 57 specimens of *B. cantabrigensis* (Davidson) from the Upper Aptian, of Upware, Cambridge and 85 specimens of the same species from Brickhill, Buckinghamshire and one specimen of "*R*" *gibbsiana* (J. de C. Sow.) from Folkestone, Kent, all in the British Museum (Natural History).

CONCLUSION

Although, externally, *Cyclothyris* shows considerable variation both in size, outline and ornament, internally it remains fairly constant. Within certain limits internal variation can be confined to the development of the hinge-plates, dental lamellae and the septum in the brachial valve. In the typical form from the Upper Aptian the dental lamellae are postero-anteriorly shorter than those of the Albian and Cenomanian forms and the hinge-plates in the Upper Aptian and Albian forms tend to be more acutely deflected towards the ventral valve than in the Cenomanian species, though this may be a variable character.

Some authors, such as Makridin (1955) and Dacqué (1934) have suggested that the genus ranges from the Upper Jurassic to Cretaceous. Their definition of the genus is most probably based on Central European material which may have contained early ancestral forms.

The Neocomian genus *Lepidorhynchia* Burri (1956) certainly has both external and internal characters in common with *Cyclothyris*. The cyclothyrid deltidial plates are already evident and the ornament of subangular costae shows a tendency to marginal dichotomy, a character observed in very young specimens of *C. latissima* from Faringdon. Also, in *Lepidorhynchia*, are seen the ventrally curved and terminally divided hinge-plates which, when further developed in *Cyclothyris*, form the main distinguishing characters allowing the genus to be separated from *Sulcirhynchia* and *Lamellaerhynchia*. Both these genera, however, have a great deal in common with *Cyclothyris* and have obviously been developed from the same original stock.

It was at first thought that *Cyclothyris* gave rise to the Upper Cretaceous genus *Cretirhynchia* but, in the light of present knowledge, this theory is no longer tenable. In his description of the genus *Cretirhynchia*, Pettitt (1950) remarked on the differences between his genus from the Upper Chalk, and the Lower Cretaceous genus *Cyclothyris*. In the same work (p. 11, text-fig. 4) he figured a series of serial sections of the type-species *C. plicatilis* (J. Sowerby) from Northfleet, Kent showing the strong converging dental lamellae, short hinge-plates persistent septum and broad radulifer crura. Recently, the writer, has prepared several serial sections of other species of *Cretirhynchia* from Norfolk and Kent which compare favourably with Pettitt's illustrations. These sections show quite clearly that *Cretirhynchia* is not a direct development of

Cyclothyris but is closely related to early Cretaceous forms represented by the species " *Rhynchonella* " *cantabrigensis* Davidson from Upware and Brickhill and " *R.*" *leightonensis* Walker from the Shenley Limestone. Both these species are here referred to *Burrirhynchia* gen. nov.

A comparison between the serial sections of *Burrirhynchia cantabrigensis* from Upware (Text-fig. 10) and *Cretirhynchia norvicensis* Pettitt from Norfolk (Text-fig. 9) shows that the two have much in common. Neither species has a pedicle collar; the outline in transverse section is similar; both have narrow thickened hinge-plates. The median septum in the brachial valve of both forms persists for well over one half the length of the shell. In addition the broad radulifer crura are given off dorsally from similarly shaped crural bases. Externally also the two forms are much alike. Both have a short, massive umbo with small foramen and ornament of fine, rounded costae. Neither species shows any of the distinguishing characters of *Cyclothyris* nor is there any tendency to asymmetry of the anterior margin, a common feature of some *Cyclothyris* species.

It is probable, therefore, that *Cretirhynchia* developed from such early Cretaceous forms as *Burrirhynchia cantabrigensis* and *B. leightonensis* which marked the beginning or early stages and *C. norvicensis* the last or later stages of its evolution. Both *B. cantabrigensis* and *B. leightonensis* are closely related to *Sulcirhynchia* Burri, from the Neocomian of Switzerland.

Cyclothyris probably died out in the Upper Cenomanian with *C. compressa* (Valenciennes *in* Lamarck), though Turonian species such as " *Rhynchonella* " *vespertilio* (Brocchi) which may have been developed from *C. compressa* and " R." *elegans* Hanstein, from the Ciply Chalk, have still to be investigated.

ACKNOWLEDGMENTS

I am greatly indebted to Dr. E. I. White, F.R.S., Keeper of Palaeontology, British Museum (Natural History) for permission to work on the collections in his department and to Dr. H. M. Muir-Wood for her kind help and encouragement, and for reading the manuscript.

My thanks are also due to Dr. F. Burri, Basel; to Mme. A. Schnorf, Musée Geologique, Lausanne, Switzerland; to Mr. A. G. Brighton and Dr. Colin Forbes, Sedgwick Museum, Cambridge; to Mr. K. J. Evans, King's College, London and to Dr. W. T. Dean and Mr. F. M. Wonnacott, British Museum (Natural History), London.

REFERENCES

AGER, D. V. 1958. *A Monograph of the British Liassic Rhynchonellidae,* **2** : 51–84, pls. 1–3. [Mon. Palaeont. Soc., London.]

D'ARCHIAC, A. 1847. Rapport sur les fossiles du Tourtia. *Mém. Soc. géol. Fr.*, Paris (2) **2** : 291–351, pls. 13–25.

BARROIS, C. 1875. Sur le Gault et sur les couches entre lesquelles il est compris dans le bassin de Paris. *Ann. Soc. géol. Nord,* Lille, **2** : 1–63.

BROCCHI, G. 1814. *Conchiologia fossile subapennina,* **2** : 241–712, pls. 1–16. Milan.

BRONGNIART, A. 1822. *In* Cuvier, G. & Brongniart, A. *Description géologique des environs de Paris.* iv + 428 pp., 11 pls. Paris.

Buckman, S. S. 1906. Brachiopod Nomenclature. *Ann. Mag. Nat. Hist.*, London (7) **18** : 32–327.

—— 1918. Brachiopoda of the Namyau Beds, Northern Shan States, Burma. *Palaeont. Indica,* Calcutta (n.s.) **3**, 2 : 1–299, pls. 1–21.

Burri, F. 1956. Die Rhynchonelliden der Unteren Kreide (Valanginien-Barremien) im westschweizerischen Juragebirge. *Ecl. geol. Helv.*, Lausanne, **49** : 600–701, pls. 1–15.

Casey, R. 1961. The stratigraphical palaeontology of the Lower Greensand. *Palaeontology,* London, **3** : 487–621, pls. 77–84.

Cayeux, L. 1949. Essai de classification des mollusques brachiopodes de l'étage cénomanien de la région. *Bull. Soc. géol. Normandie,* Le Havre (n.s.) **3** : 1–4.

Clerc, M. & Favre, J. 1918. *Catalogue illustré de la collection Lamarck, Part I.* 117 pls. Paris.

Cooper, G. A. 1955. New Cretaceous Brachiopoda from Arizona. *Smithson. Misc. Coll.*, Washington, **131**, 4 : 1–18, pls. 1–4.

Corroy, G. 1925. Le Néocomien de la bordure orientale du Bassin de Paris. *Bull. Soc. Sci nat. Nancy* (4) **2** : 1–171.

Dacqué, E. 1934. Wirbellose des Jura. *In* Gurich, G. *Leitfossilien,* **7** : 582 pp., 24 pls. Berlin.

Dall, W. H. 1877. Index to the names which have been applied to subdivisions of the Class Brachiopoda. *Bull. U.S. Nat. Mus.*, Washington, **8** : 1–87.

Davidson, T. 1852–54. *A Monograph of British Cretaceous Brachiopoda,* **2**. 117 pp., 12 pls. [Mon. Palaeont. Soc., London.]

—— 1874. *A Monograph of the British Fossil Brachiopoda,* **4**, 1. *Supplement to the Recent, Tertiary, and Cretaceous Species.* 72 pp., 8 pls. [Mon. Palaeont. Soc., London.]

Defrance, M. J. L. 1828. *Terebratula deformis* Lamk. *Dict. Sci. nat.*, Paris, **53** : 160.

Fage, G. 1935. Rhynchonelles du Crétacé Supérieur des Charentes. *Bull. Soc. géol. Fr.*, Paris (5) **4** : 433–441, pl. 1.

Fitton, J. 1836. Observations on some of the strata between the Chalk and the Oxford Oolite in south-east of England. *Trans. Geol. Soc. Lond.* (2) **4** : 335–349, pls. 11–23.

Geinitz, H. B. 1872. Das Elthalgebirge in Sachsen. *Palaeontographica,* Stuttgart, **20** : 147–207, pls. 36–45.

Hanstein, R. von. 1879. *Brachiopoden der oberen Kreide von Ciply.* 58 pp. Bonn.

Hertlein, L. G. & Grant, U. S. 1944. The Cenozoic Brachiopoda of Western North America. *Univ. Calif. Publ. Math. Phys. Sci.*, Berkeley, **3**. vi + 236 pp., 21 pls.

Imlay, R. 1937. Lower Neocomian fossils from the Miquihuana region, Mexico. *J. Paleont.*, Menasha, **11** : 552–574, pls. 1–13.

Jukes-Browne, A. J. 1900. *Cretaceous Rocks of Britain,* 1. *Gault and Upper Greensand of England.* x + 499 pp. [Mem. Geol. Surv. U.K.] London.

—— & Hill, W. 1896. A Delimitation of the Cenomanian; being a comparison of the corresponding Beds of South-Western England and Western France. *Quart. J. Geol. Soc., Lond.*, **52** : 99–177.

Lamarck, J. P. B. 1819. *Histoire naturelle des animaux sans vertèbres,* **6**, 1 : 1–343. Paris.

Makridin, V. P. 1955. Some Jurassic Rhynchonellids of the European part of USSR. *Zap. Geol. Fak. Kharkov State Univ.*, **12** : 81–91. [In Russian].

M'Coy, F. 1844. *A synopsis of the characters of the Carboniferous Limestone fossils of Ireland.* viii + 207 pp., 29 pls. Dublin.

Meyer, C. J. A. 1874. On Cretaceous rocks of Beer Head and adjoining cliff-sections, and on the relative horizons therein of the the Warminster and Blackdown fossiliferous deposits. *Quart. J. Geol. Soc. Lond.*, **30** : 369–393.

Middlemiss, F. A. 1959. English Aptian Terebratulidae. *Palaeontology,* London, **2** : 94–142, pls. 15–18.

Muir-Wood, H. M. 1934. On the internal structure of some Mesozoic Brachiopoda. *Philos. Trans.*, London (B) **223** no. 505 : 511–567, pls. 1, 2.

MUIR-WOOD, H. M. 1955. *A History of the Classification of the Phylum Brachiopoda.* 124 pp. British Museum (Nat. Hist.), London.

—— & COOPER, G. A. 1960. Morphology, Classification and life habits of the Productoidea (Brachiopoda). *Mem. Geol. Soc. Amer.*, Rochester, N.Y., **81** : xi + 447 pp., 135 pls.

OWEN, E. F. 1955. The use of sugar solution in the differentiation of the internal structures of Upper Chalk Brachiopods. *Proc. Geol. Ass. Lond.*, **66** : 369–370.

—— 1956. The Lower Cretaceous Brachiopods " *Rhynchonella* " *gibbsiana* (J. de C. Sowerby) and *Sulcirhynchia hythensis* sp. nov. *Ann. Mag. Nat. Hist.*, London (12) **9** : 164–172, pl. 1.

—— 1960. A Note on " *Rhynchonella* " *sulcata* (Parkinson) from the Lower Cretaceous of Great Britain. *Ann. Mag. Nat. Hist.*, London (13) **2** : 248–256, pl. 1.

ORBIGNY, A. D'. 1848–51. *Terrains crétacés. Paléontologie française*, **4** : 1–390, pls. 490–599. Paris.

PETTITT, N. E. 1950. *Rhynchonellidae of the British Chalk, I.* 26 pp., 2 pls. [Mon. Palaeont. Soc., London.]

—— 1954. *Rhynchonellidae of the British Chalk, II.* 26 pp, 1 pl. [Mon. Palaeont. Soc., London].

PICTET, F. J. 1872. Description des fossiles du terrain crétacé des environs de Sainte-Croix, 5. *Matér. Paléont. suisse*, Genève (6) **1** : 1–158, pls. 195–208.

—— & ROUX, W. 1847–53. *Mollusques fossiles des grès verts de Genève.* 558 pp., 51 pls. Genève.

QUENSTEDT, F. A. 1882. *Handbuch der Petrefactenkunde.* viii + 1239 pp., Tübingen (esp. p. 696).

RZHONITSKAYA, M. A. 1959. Systematics of the Rhynchonellids. *Pal. J. Akad. Nauk. SSSR.*, **1** : 25–36. [In Russian].

SCHLOENBACH, U. 1867. Uber die Brachiopoden der norddeutschen Cenoman-Bildungen. *Geogn. Paläont. Beitr.* (*E. W. Benecke*), München, **1** : 399–506, pls. 21–23.

SCHUCHERT, C. 1913. Brachiopoda. *In* Zittel, K. A. von, edited by Eastman, C. R. *Textbook of Palaeontology*, **1** : 355–420, figs. 526–636. 2nd edit. London.

SHARPE, D. 1854. On the age of the fossiliferous sands and gravels of Farringdon and its neighbourhood. *Quart. J. Geol. Soc. Lond.*, **10** : 176–198, pls. 1, 2.

SOWERBY, J. 1812–15. *Mineral Conchology of Great Britain*, **1**. vii + 234 pp., 102 pls. London.

—— 1818–21. *Mineral Conchology of Great Britain*, **3**. 184 pp., pls. 204–306. London.

SOWERBY, J. DE C. 1836. *In* Fitton, J. Observations on some of the strata between the Chalk and the Oxford Oolite in the south-east of England. *Trans. Geol. Soc. Lond.* (2) **4** : 335–349, pls. 11–23.

SPATH, L. F. 1926. On the zones of the Cenomanian and Uppermost Albian. *Proc. Geol. Ass. Lond.*, **37** : 420–432.

THOMSON, J. A. 1927. Brachiopod morphology and genera (Recent and Tertiary). *N.Z. Board Sci. Art. Manual*, **7** : vi + 338 pp., 2 pls. Dominion Museum, Wellington.

WRIGHT, C. W. & E. V. 1951. *A survey of the fossil cephalopoda of the Chalk of Great Britain.* 41 pp. [Mon. Palaeont. Soc., London.]

PLATE 4

Figs. 1*a–c*. *Cyclothyris scaldisensis* (d'Archiac). Tourtia, Gussignies, Belgium. BM. B.11965.

Figs. 2*a–c*. *Cyclothyris dimidiata* (J. Sowerby) = *C. difformis*. Cenomanian, Halldown, south-east Devon. BM. B.61466.

Figs. 3*a–c*. *Cyclothyris antidichotoma* (Buvignier). Lower Albian, Shenley Hill, Leighton Buzzard, Bedfordshire. BM. BB.41495.

Figs. 4*a–c*. *Cyclothyris antidichotoma* (Buvignier). Lower Albian, Goudinière, Grand St. Bernard, Savoie, France. BM. BB.41486.

Figs. 5*a–c*. *Cyclothyris antidichotoma* (Buvignier). Upper Aptian, Brickhill, Buckinghamshire. BM. BB.41490.

Figs. 6*a–c*. *Cyclothyris antidichotoma* (Buvignier). Upper Aptian, Upware, Cambridge. BM. B.27264.

Figs. 7*a–c*. *Cyclothyris latissima* (J. de C. Sowerby). Upper Aptian, Faringdon, Berkshire. BM. BB. 41494.

Figs. 8*a–c*. *Cyclothyris latissima* (J. de C. Sowerby). Lectotype. Upper Aptian, Faringdon, Berkshire. BM. B.61499.

Figs. 9*a–c*. *Cyclothyris levis* sp. n. Holotype. Lower Albian, Shenley Hill, Leighton Buzzard, Bedfordshire. BM. BB.41493.

Figs. 10*a–c*. *Cyclothyris lepida* sp. n. Holotype. Upper Aptian, Brickhill, Buckinghamshire. Sedgwick Museum Coll. B.25683.

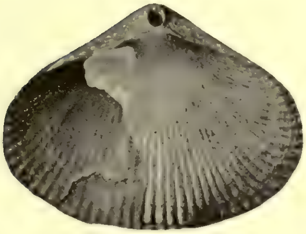
Figs. 11*a–c*. *Cyclothyris depressa* (J. de C. Sowerby). Lectotype. Upper Aptian, Faringdon, Berkshire. BM. B.61468.

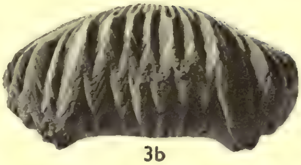
Figs. 12*a–c*. *Cyclothyris schloenbachi* (Davidson). Lectotype. Lower Cenomanian, Shaftesbury, Wiltshire. BM. B.8216.

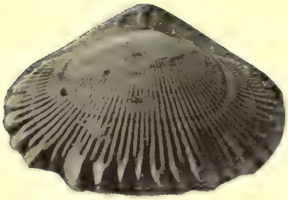
Figs. 13*a–c*. *Cyclothyris schloenbachi* (Davidson). Coarsely costate variant from Chardstock, Somerset. BM. B. 8215.

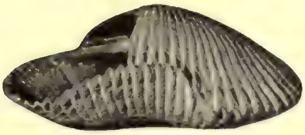
All figures at natural size unless otherwise stated.
BM. = British Museum (Natural History).

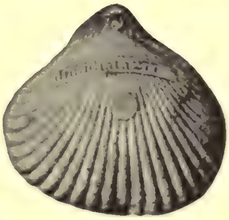
4 JUN 1962

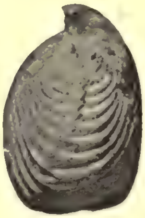

1a

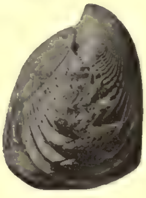

3b

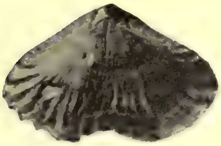

3a

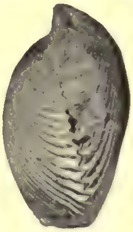

1b

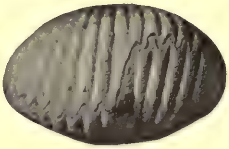

2a

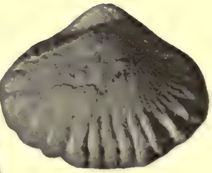

2c

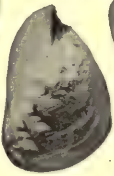

3c

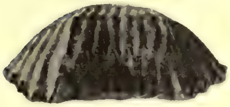

4a

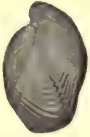

1c

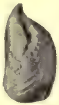

2b

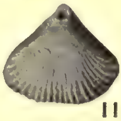

5a

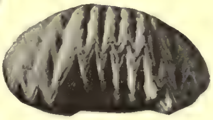

5c

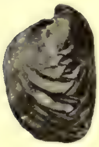

4b

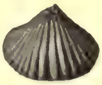

7c

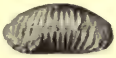

11c

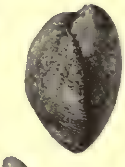

11a

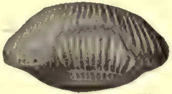

5b

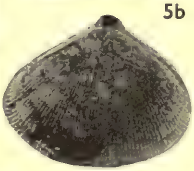

4c

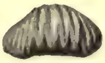

13a

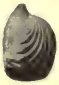

11b

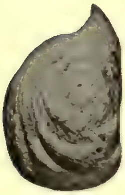

9c

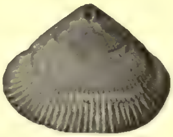

7b

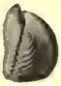

9a

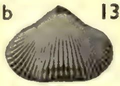

13b

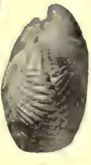

13c

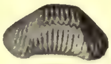

6c

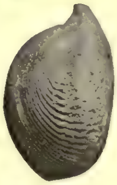

7a

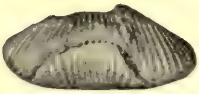

12c

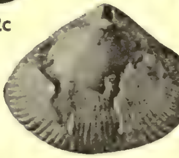

12a

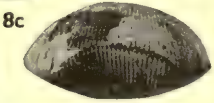

8c

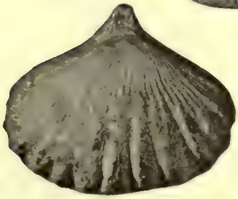

12b

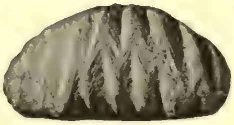

10c

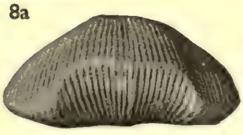

8b


8a


9b


6a


6b


10b

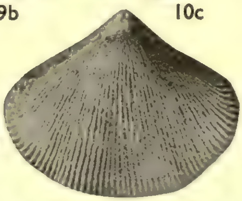

10a

PLATE 5

FIGS. 1*a–c*. *Cyclothyris difformis* (Valenciennes *in* Lamarck). Cenomanian, Warminster, Wiltshire. Typical form. B.M. no. 45336.

FIGS. 2*a–c*. *Cyclothyris difformis* (Valenciennes *in* Lamarck). Lower Cenomanian, Wilmington, south Devon. BM. BB.41433.

FIGS. 3*a–c*. *Cyclothyris difformis* (Valenciennes *in* Lamarck). Lower Cenomanian, Cap le Hève, near Le Havre, Normandy BM. B.82754.

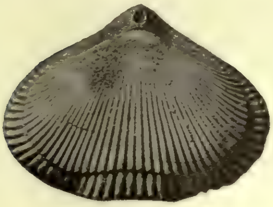
FIGS. 4*a–c*. *Cyclothyris difformis* (Valenciennes *in* Lamarck). Lower Cenomanian, Wilmington, south Devon. BM. BB.15292.

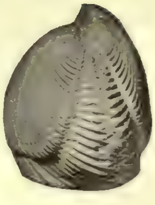
FIGS. 5*a–c*. *Cyclothyris difformis* (Valenciennes *in* Lamarck). Tourtia, Tournai, Belgium. BM. BB.41476.

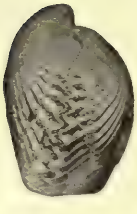
FIGS. 6*a–c*. *Cyclothyris difformis* (Valenciennes *in* Lamarck). Cenomanian, Essen, Germany. Similar variant to fig. 5 from Belgium. BM. BB.41473.

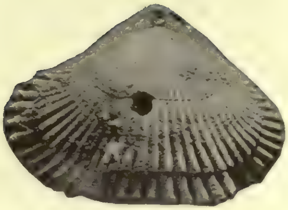
FIGS. 7*a–c*. *Cyclothyris difformis* (Valenciennes *in* Lamarck). Lower Cenomanian, Warminster, Wiltshire. BM. B.8301.

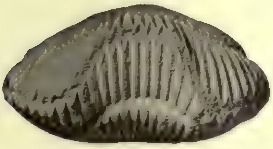
FIGS. 8*a–c*. *Cyclothyris compressa* (Valenciennes *in* Lamarck). Upper Cenomanian, Le Mans, Sarthe, France. BM. BB.41489.

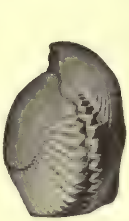

1a

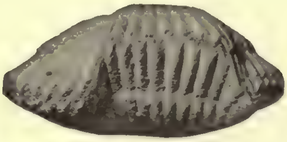

1c

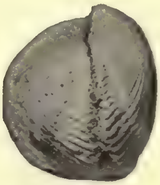

2c

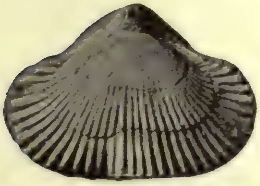

2a

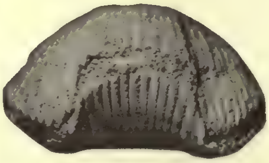

1b

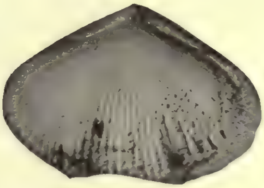

3c

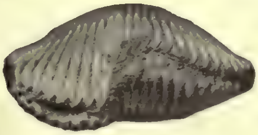

2b

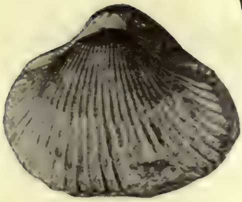

4c

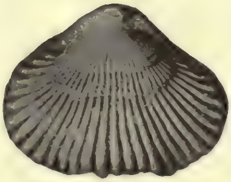

3a

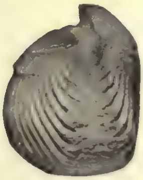

4b

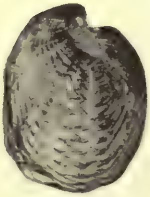

4a

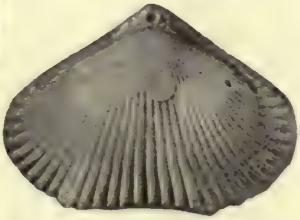

3b

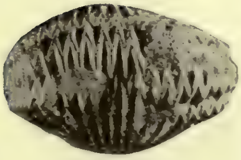

5a

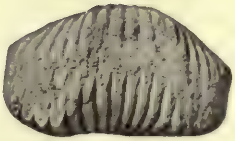

6a

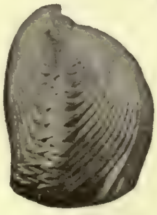

6c

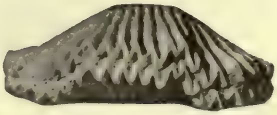

5c

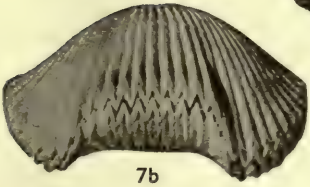

7a

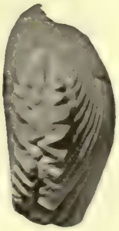

5b

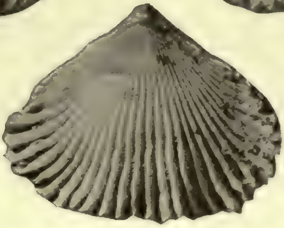

6b


7c


8b


7b


8c


8a

THE TRILOBITES OF THE CARADOC SERIES IN THE CROSS FELL INLIER OF NORTHERN ENGLAND

W. T. DEAN

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 7 No. 3
LONDON: 1962

THE TRILOBITES OF THE CARADOC SERIES IN THE CROSS FELL INLIER OF NORTHERN ENGLAND

BY

WILLIAM THORNTON DEAN

Pp. 65–134 ; *Pls.* 6–18 ; 5 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 7 No. 3
LONDON : 1962

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical Series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

This paper is Vol. 7, *No.* 3 *of the Geological (Palaeontological) series.*

© Trustees of the British Museum 1962

PRINTED BY ORDER OF THE TRUSTEES OF
THE BRITISH MUSEUM

Issued August 1962 *Price Forty-two Shillings*

THE TRILOBITES OF THE CARADOC SERIES IN THE CROSS FELL INLIER OF NORTHERN ENGLAND

By WILLIAM THORNTON DEAN

Page

I. INTRODUCTION AND ACKNOWLEDGMENTS 69
II. STRATIGRAPHICAL SUMMARY 69
III. SYSTEMATIC DESCRIPTIONS 72
  Family Raphiophoridae Angelin 72
    Lonchodomas swindalensis sp. nov. 72
    Lonchodomas pennatus (La Touche) 78
  Family Trinucleidae Hawle & Corda 79
   Subfamily Cryptolithinae Angelin 79
    Broeggerolithus nicholsoni (Reed) 79
    Broeggerolithus melmerbiensis sp. nov. 81
    Broeggerolithus cf. *transiens* (Bancroft) 82
    Broeggerolithus sp. 83
    Onnia gracilis (Bancroft) 84
    Onnia superba (Bancroft) *pusgillensis* Dean 84
   Subfamily Tretaspidinae Whittington 85
    Tretaspis cf. *ceriodes donsi* Størmer 85
    Tretaspis convergens Dean 85
    Tretaspis kiaeri Størmer *radialis* Lamont 86
    Tretaspis kiaeri Størmer *duftonensis* Dean 86
  Family Cheiruridae Salter 86
   Subfamily Cyrtometopinae Öpik 86
    Pseudosphaerexochus cf. *octolobatus* (M'Coy) 87
  Family Encrinuridae Angelin 88
   Subfamily Encrinurinae Angelin 88
    Encrinurus sp. 88
   Subfamily Dindymeninae Přibyl 89
    Dindymene duftonensis sp. nov. 89
    Dindymene sp. 90
   Subfamily Cybelinae Holliday 91
    Atractopyge scabra sp. nov. 91
    Atractopyge? sp. 93
    Paracybeloides cf. *girvanensis* (Reed) 94
    Paracybeloides sp. 95
  Family Dalmanitidae Reed 95
   Subfamily Dalmanitinae Reed 95
    Dalmanitina mucronata (Brongniart) *matutina* subsp. nov. . 95
   Subfamily Acastinae Delo 97
    Kloucekia (*Phacopidina*) *apiculata* (M'Coy) 97
    Duftonia lacunosa Dean 97

Page
Family Pterygometopidae Reed 98
Subfamily Pterygometopinae Reed 98
Calyptaulax planiformis sp. nov. 98
Estoniops alifrons (M'Coy) 100
Subfamily Chasmopsinae Pillet 104
Chasmops cf. *extensa* (Boeck) 104
Chasmops aff. *maxima* (Schmidt) 105
Chasmops sp. 105
Family Homalonotidae Chapman 106
Brongniartella minor (Salter) 106
Brongniartella ascripta (Reed) 106
Brongniartella bisulcata (M'Coy) 108
Brongniartella depressa sp. nov. 108
Brongniartella aff. *platynota* (Dalman) 110
Family Calymenidae Burmeister 111
Flexicalymene cf. *caractaci* (Salter) 114
Onnicalymene onniensis (Shirley) 115
Onnicalymene laticeps (Bancroft) 115
Diacalymene cf. *marginata* Shirley 116
Gravicalymene jugifera sp. nov. 116
Family Dimeropygidae Hupé 118
Toernquistia aff. *reedi* Thorslund 118
Family Illaenidae Hawle & Corda 120
Stenopareia? sp. 120
Family Lichidae Hawle & Corda 120
Subfamily Homolichinae Phleger 120
Conolichas melmerbiensis (Reed) 120
Platylichas cf. *laxatus* (M'Coy) 121
Family Odontopleuridae Burmeister 122
Primaspis semievoluta (Reed) 122
Odontopleurid gen. et sp. ind. 123
Family Otarionidae R. &. E. Richter 123
Otarion sp. 123
Family Proetidae Salter 124
Subfamily Proetidellinae Hupé 124
Proetidella? marri sp. nov. 124
Family Remopleurididae Hawle & Corda 127
Remopleurides spp. 127
IV. STRATIGRAPHICAL DISTRIBUTION AND RELATIONSHIPS OF THE TRILOBITES 128
V. REFERENCES 130

SYNOPSIS

The trilobites known from the Caradoc Series in the Cross Fell Inlier are described and figured, many of them for the first time. They comprise fifty species and subspecies, assigned to twenty-eight genera and fifteen families. The relationships of the trilobites to those of other successions is reviewed. In the Longvillian and Marshbrookian Stages the fauna is of Anglo-Welsh type with occasional Baltic elements, but in subsequent stages the affinities with corresponding Norwegian and Swedish faunas becomes marked, reaching a maximum in the Pusgillian Stage.

I. INTRODUCTION AND ACKNOWLEDGMENTS

THE name Cross Fell Inlier is applied by geologists to the elongated area of Lower Palaeozoic rocks, a few miles north of Appleby, Westmorland, which extends in a south-south-easterly direction between the Carboniferous strata of the Pennines and the Permo-Trias of the Vale of Eden. The geological structure of the area is of great complexity and has been described by Shotton (1935). The disposition of the principal outcrops of Caradoc strata is shown in Text-fig. 1.

Although the first detailed stratigraphical accounts, accompanied by faunal lists, of the Caradoc Series in the Inlier were given during the last century by Harkness & Nicholson (1878), and Nicholson & Marr (1891), it was not until 1907 and 1910 that any figures and descriptions of trilobites were published. In those years Reed described four new species, *Lichas melmerbiensis*, *Acidaspis semievoluta*, *Homalonotus ascriptus* and *Trinucleus nicholsoni*, from strata which he called Dufton Shales at the road-section near Melmerby, as well as listing several other species from the same locality.

Bancroft (1933) listed a few Shropshire species of trilobites and brachiopods from the Inlier but it was not until 1936 that another trilobite was illustrated, when Shirley figured a specimen of *Flexicalymene onniensis*, a south Shropshire species, from an unspecified locality and horizon within the Dufton Shales of Pus Gill, near Dufton. In 1948 Bancroft's manuscript notes on the Cross Fell succession, including locality maps of Swindale Beck and part of Pus Gill, were published posthumously by Lamont, who added photographs of certain Shropshire specimens but figured none from the Inlier.

Since then a new genus, *Duftonia*, has been described from the Dufton Shales by the writer (Dean, 1959) who, in a later paper (1959*a*), discussed the detailed stratigraphy of the area and gave faunal lists. More recently some of the Trinucleidae occurring in the upper part of the succession have been described and figured (Dean, 1961). The present work aims at describing and figuring all the trilobites listed and discussed in the foregoing papers. Extensive collections of trilobites have been made during field-work financed in part by grants from the Gloyne Fund of the Geological Society of London, and I am grateful to the Council of the Society for their assistance. All the material is housed in the British Museum (Natural History), London. I wish to thank the Council of the Yorkshire Geological Society for permission to reproduce the sketch-map shown in Text-fig. 4. I am indebted to Mr. A. G. Brighton for the loan of type-specimens from the Sedgwick Museum, Cambridge, to my wife for her important share of the collecting, and to Professor W. F. Whittard who has kindly read and criticized the manuscript.

II. STRATIGRAPHICAL SUMMARY

The following table represents the subdivisions of the Caradoc Series which are generally recognized today in the main portion of the Inlier, together with the equivalent faunal zones as established in the type-area of south Shropshire.

The subdivision of the strata into Corona Beds and Dufton Shales is made on lithological grounds, the former including maroon and grey mudstones and shales

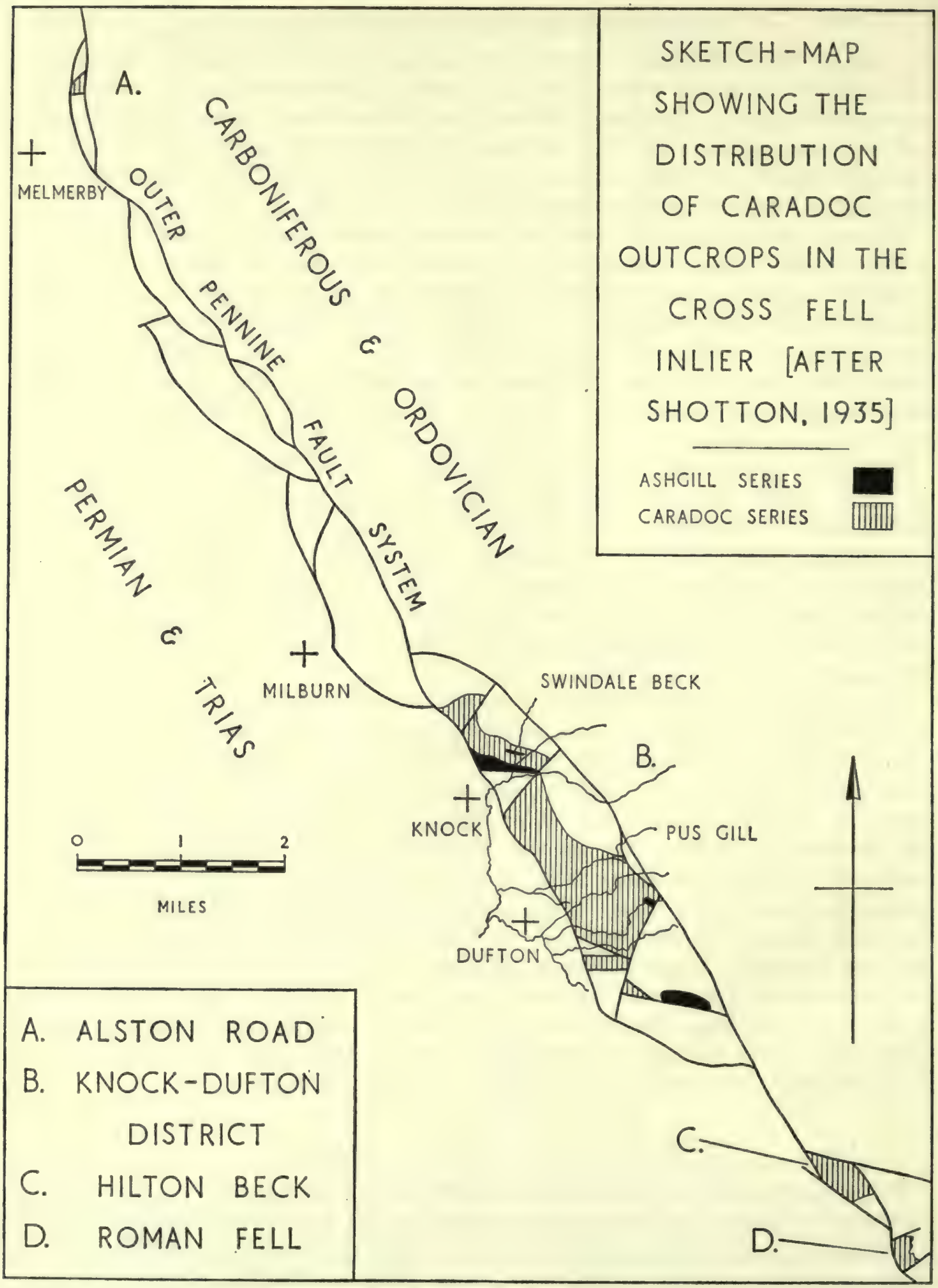

SKETCH-MAP SHOWING THE DISTRIBUTION OF CARADOC OUTCROPS IN THE CROSS FELL INLIER [AFTER SHOTTON, 1935]
ASHGILL SERIES ■
CARADOC SERIES ▥
A.
MELMERBY
CARBONIFEROUS & ORDOVICIAN
OUTER PENNINE FAULT SYSTEM
PERMIAN & TRIAS
MILBURN
SWINDALE BECK
B.
KNOCK
PUS GILL
DUFTON
0
1
2
MILES
C.
D.
A. ALSTON ROAD
B. KNOCK-DUFTON DISTRICT
C. HILTON BECK
D. ROMAN FELL

Fig. 1.

Stage		Zonal Trilobite	Zonal Brachiopod	Lithological Subdivision
Pusgillian		—	—	Dufton Shales
Onnian		*Onnia superba*	—	
		Onnia gracilis	*Onniella broeggeri*	
		Onnia ? cobboldi	*Onniella inconstans*	
Actonian		*Platylichas laxatus*	*Cryptothyris paracyclica*	
Marshbrookian		*Broeggerolithus transiens*	*Onniella reuschi* *Dalmanella unguis* *Dalmanella wattsi*	
Longvillian	U	*Broeggerolithus longiceps*	*Kjaerina typa* *Kjaerina bipartita*	
	L	*Broeggerolithus globiceps*	*Bancroftina typa* *Dalmanella indica* and *D. lepta* *Dalmanella horderleyensis ?*	Corona Beds

with occasional limestone bands, whilst the latter comprise essentially a rather monotonous series of dark-grey mudstones and shales with bands of nodular and impure limestone which often weather to a rotten-stone or "gingerbread" rock. The Corona Beds are shown in the table to coincide with the limits of the Lower Longvillian Substage, but in fact the zone of *Dalmanella indica* and *D. lepta* is the lowest faunal horizon definitely recognized, though the underlying zone may well be represented. The topmost zone of the Lower Longvillian is represented in the highest Corona Beds and it seems likely that there is a transition to the overlying Dufton Shales, but owing to extensive faulting the lowest zone of the Upper Longvillian has not been detected throughout the greater part of the Inlier. The remainder of the succeeding Caradoc strata as found in the Shropshire type-area are, for the most part, represented in the Cross Fell Inlier, with the addition of the Pusgillian Stage. This subdivision is held to constitute the topmost part of the Caradoc Series and to pre-date any known Ashgill strata. In Swindale Beck, near Knock, the Pusgillian is followed in the succession by the *Staurocephalus* or Swindale Limestone. The junction of the two has often been assumed to be conformable, but the writer believes there is a marked stratigraphical break above the Pusgillian, and that the Limestone represents a relatively high Ashgill horizon, as it is followed at Swindale Beck by Ashgill Shales with *Hirnantia sagittifera* (M'Coy). South-east of Dufton the Pusgillian outcrop is separated from that of the Swindale Limestone by a small thickness of strata, equated with part of the *Diacalymene* Beds of Cautley, which are probably overstepped by the Limestone.

The northernmost outcrops of Caradoc strata within the Inlier occur only in the vicinity of the village of Melmerby, after which they are known as the Melmerby Beds. The rocks have been divided into an upper and lower series; the Upper

Melmerby Beds contain a fauna indicative of the lower zone of the Upper Longvillian Substage, an horizon which, as stated earlier, is not yet known elsewhere in the Inlier. In the field, the Lower Melmerby Beds appear to underlie the upper beds stratigraphically and are considered to be of Lower Longvillian age ; they contain abundant evidence of a Longvillian age but the zonal brachiopods of the Shropshire succession have not yet been detected and may be absent owing to the unsuitability of the environment. The rocks are mainly dark-green or maroon, blocky mudstones with occasional impure, nodular limestones. Their fauna includes a conspicuously large number of trinucleid trilobites, accompanied by common *Kloucekia apiculata* (M'Coy), features which readily distinguish them from the equivalent strata farther south in the Inlier, and which are more suggestive of corresponding North Welsh faunas.

No useful evidence has yet been obtained from the region to elaborate on the correlation between the shelly and graptolitic successions already put forward for south Shropshire (Dean, 1958 : 226). The Pusgillian, from its position above the Onnian (believed to represent the topmost *Dicranograptus clingani* Zone), is equated approximately with the *Pleurograptus linearis* Zone, and the shelly fauna suggests a correlation with Etage 4cα of southern Norway, an horizon which is itself correlated with that graptolite zone.

The fossil localities cited in the following descriptions are shown in Text-figs. 2–5. Text-fig 3 covers the well-known section of Swindale Beck, just north-east of the village of Knock ; Text-fig 2 shows Pus Gill, north-east of Dufton ; Text-fig. 4 covers the large area of east of Dufton, with the important sections of Dufton Town Sike, Billy's Beck and Harthwaite Sike ; Text-fig. 5 shows the small, isolated outcrop of the Melmerby Beds north-east of Melmerby, near the northern end of the Inlier.

III. SYSTEMATIC DESCRIPTIONS

Family RAPHIOPHORIDAE Angelin, 1854

Genus ***LONCHODOMAS*** Angelin, 1854

TYPE-SPECIES. *Ampyx rostratus* Sars, 1835 by subsequent designation of Bassler (1915 : 41).

Lonchodomas swindalensis sp. nov.

(Pl. 6, figs. 2, 6, 8)

1959*a*. *Lonchodomas* aff. *rostratus* (Sars) Dean, pp. 194, 207.

DIAGNOSIS. *Lonchodomas* with glabella projecting only short distance in front of fixigenae. Pygidium semi-elliptical with four pairs of pleural furrows, the first pair being the most sharply defined.

DESCRIPTION. The material is fragmentary for the most part but includes two almost whole cranidia and one small, well-preserved pygidium. Excluding the

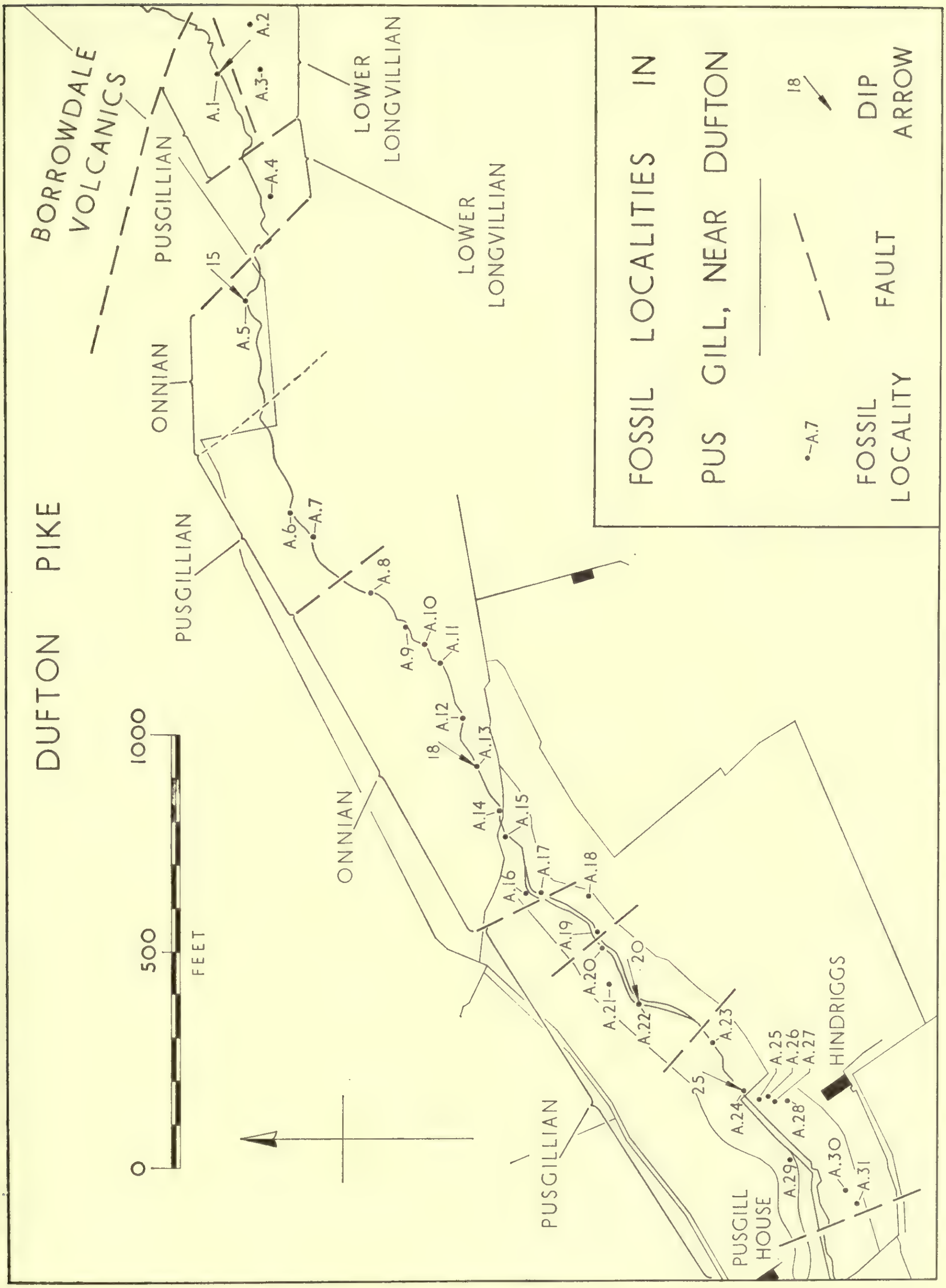

FOSSIL LOCALITIES IN
PUS GILL, NEAR DUFTON
•—A.7 FOSSIL LOCALITY
FAULT
18 DIP ARROW
DUFTON PIKE
BORROWDALE VOLCANICS
PUSGILLIAN
LOWER LONGVILLIAN
ONNIAN
HINDRIGGS
PUSGILL HOUSE
0
500
1000
FEET
A.1
A.2
A.3
A.4
15
A.5
A.6
A.7
A.8
A.9
A.10
A.11
A.12
18
A.13
A.14
A.15
A.16
A.17
A.18
A.19
A.20
20
A.21
A.22
A.23
25
A.24
A.25
A.26
A.27
A.28
A.29
A.30
A.31

Fig. 2.

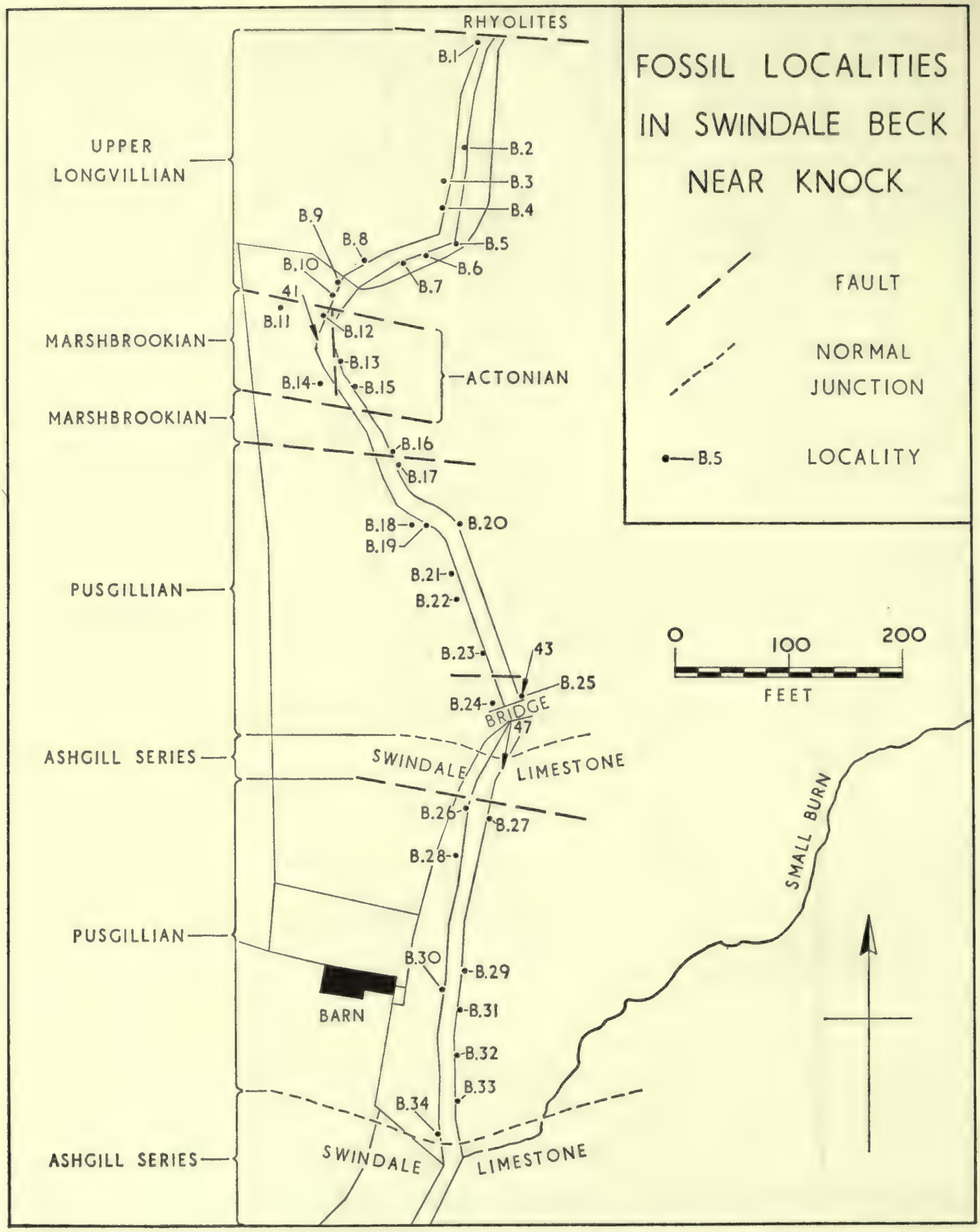

FOSSIL LOCALITIES IN SWINDALE BECK NEAR KNOCK
FAULT
NORMAL JUNCTION
B.5 LOCALITY
RHYOLITES
UPPER LONGVILLIAN
MARSHBROOKIAN
ACTONIAN
MARSHBROOKIAN
PUSGILLIAN
ASHGILL SERIES
PUSGILLIAN
ASHGILL SERIES
B.1
B.2
B.3
B.4
B.5
B.6
B.7
B.8
B.9
B.10
41
B.11
B.12
B.13
B.14
B.15
B.16
B.17
B.18
B.19
B.20
B.21
B.22
B.23
43
B.25
B.24
BRIDGE
47
SWINDALE LIMESTONE
B.26
B.27
B.28
B.30
B.29
BARN
B.31
B.32
B.33
B.34
SWINDALE LIMESTONE
SMALL BURN
0
100
200
FEET

FIG. 3.

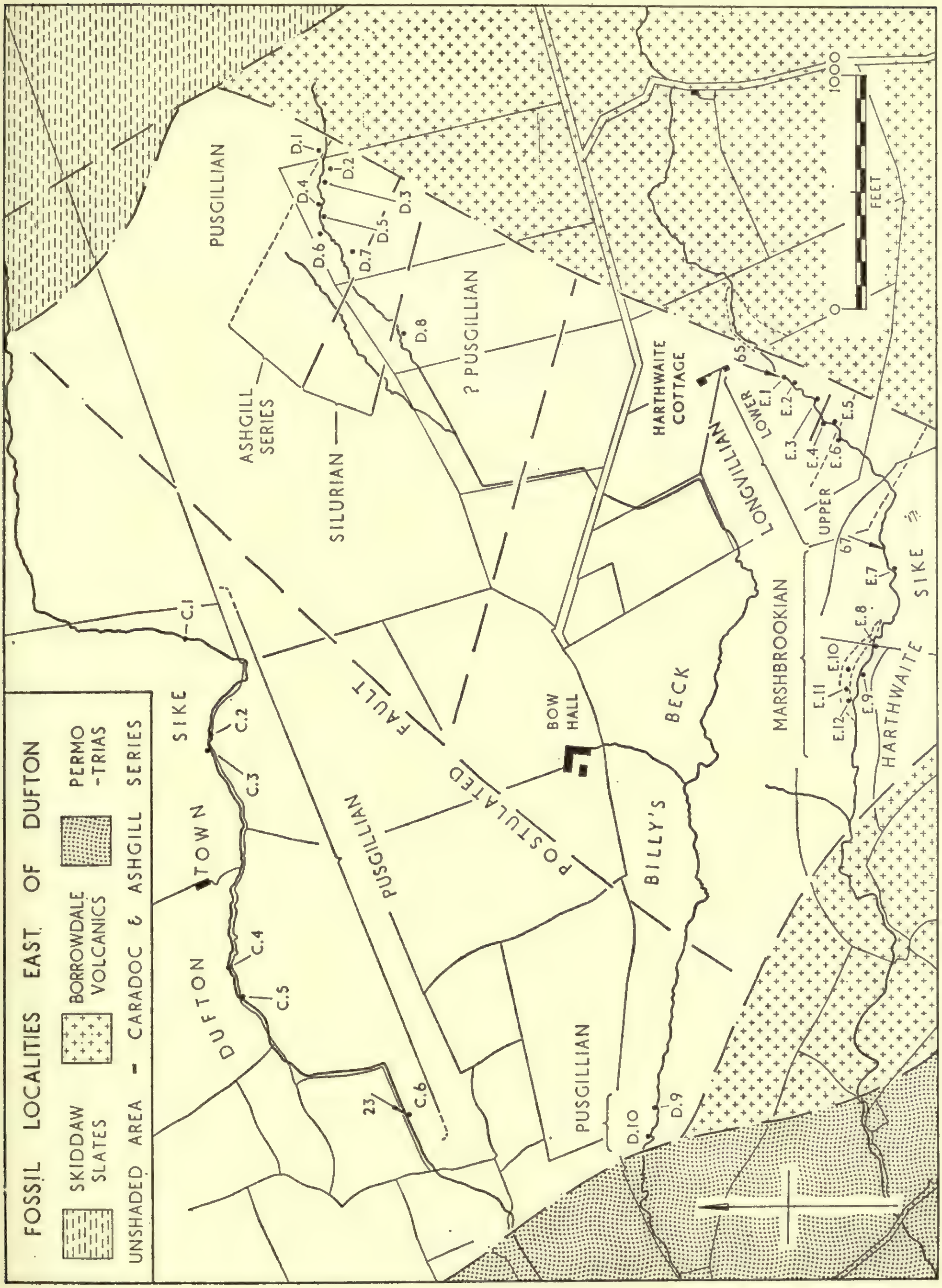

FOSSIL LOCALITIES EAST OF DUFTON
SKIDDAW SLATES
BORROWDALE VOLCANICS
PERMO -TRIAS
UNSHADED AREA - CARADOC & ASHGILL SERIES
DUFTON TOWN SIKE
C.1
C.2
C.3
C.4
C.5
C.6
23
PUSGILLIAN
PUSGILLIAN
PUSGILLIAN
? PUSGILLIAN
ASHGILL SERIES
SILURIAN
D.1
D.2
D.3
D.4
D.5
D.6
D.7
D.8
D.9
D.10
POSTULATED FAULT
BOW HALL
BILLY'S BECK
HARTHWAITE COTTAGE
LOWER LONGVILLIAN
UPPER
65
67
E.1
E.2
E.3
E.4
E.5
E.6
E.7
E.8
E.9
E.10
E.11
E.12
MARSHBROOKIAN
HARTHWAITE SIKE
0
FEET
1000

Fig. 4.

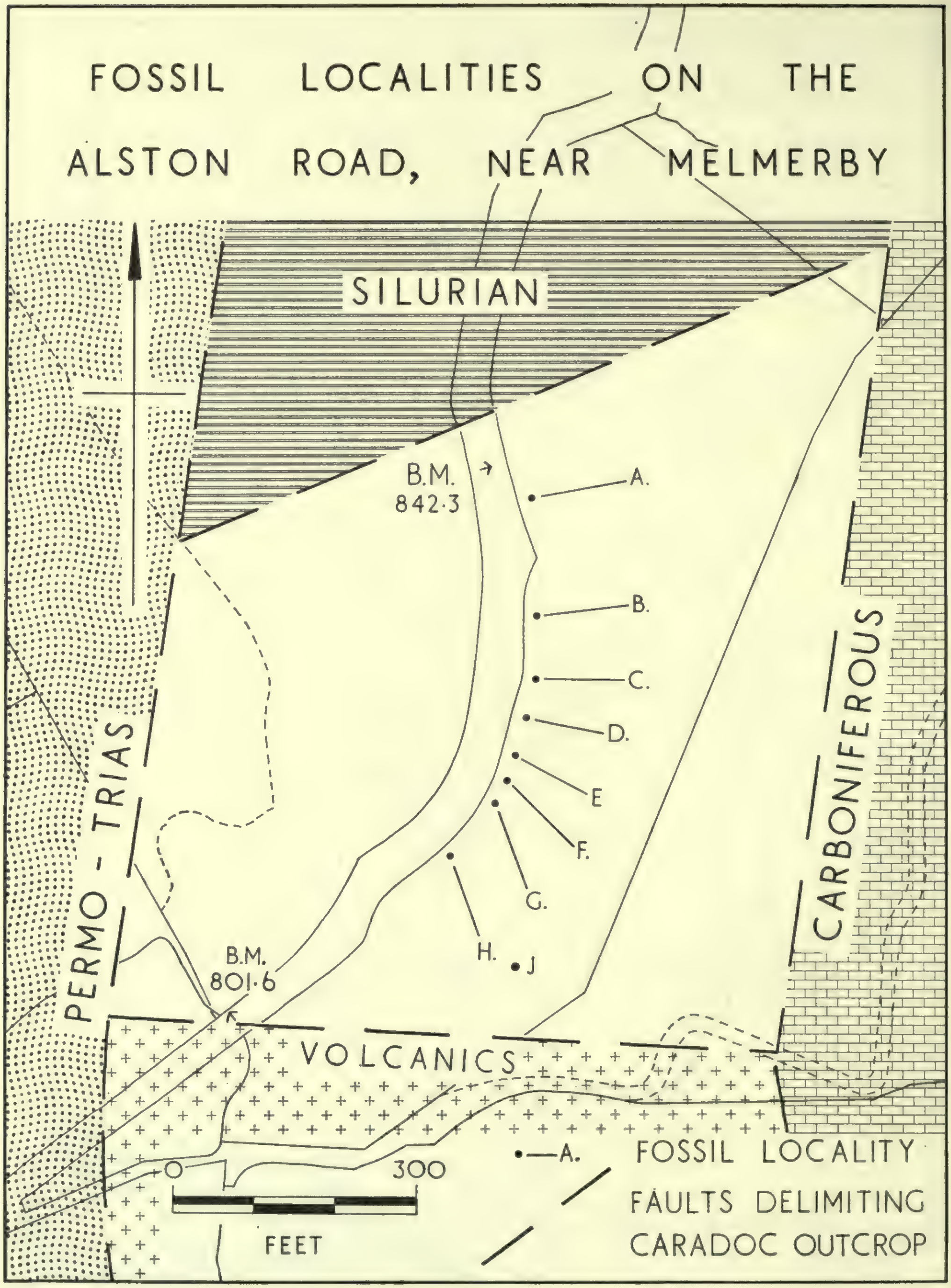

FOSSIL LOCALITIES ON THE ALSTON ROAD, NEAR MELMERBY
SILURIAN
PERMO - TRIAS
CARBONIFEROUS
VOLCANICS
B.M. 842·3
B.M. 801·6
A.
B.
C.
D.
E
F.
G.
H.
J
0
300
FEET
A. FOSSIL LOCALITY
FAULTS DELIMITING CARADOC OUTCROP

Fig. 5.

frontal spine, the dimensions of the cranidia, numbered respectively In. 49946 and In. 49968, are as follows: length, 5 mm., breadth, 9 mm.; length, 11 mm.; breadth, 16 mm. Dimensions of the pygidium, In. 49967, are: length, 1·5 mm., breadth, 4·5 mm. The cranidium is roughly rhomboidal in plan, produced anteriorly into a long, frontal spine, the surface of which bears fine, longitudinal striae. The glabella attains its greatest breadth at its mid-point and is bounded by almost straight axial furrows containing slot-like hypostomal pits, situated frontally. One cranidium (Pl. 6, fig. 2) shows a faint median ridge extending from near the occipital furrow to the base of the frontal spine, where it is replaced by a groove; similar grooves occur on the sides and undersurface of the frontal spine as in other species of *Lonchodomas*, giving rise to the fluted, quadrate cross-section characteristic of the genus. The posterior margin of the cranidium, and the pleuroccipital furrows are parallel, transversely straight except medially where, owing to a small extension of the glabella, they are convex backwards.

The pygidium is semi-elliptical in outline with a strongly-curved, steeply-declined, posterior border which carries fine, parallel terrace lines, though the latter are not visible in the photograph (Pl. 6, fig. 6). The anterior margin is straight medially but curves forwards a little anterolaterally. There are four pairs of pleural furrows, the first pair being the most deeply impressed; all are deepest anterolaterally becoming faint at, or near, the shallow axial furrows. No axial rings are visible.

HORIZON AND LOCALITIES. All the known specimens have been collected from Dufton Shales belonging to the upper half of the Upper Longvillian Substage in Swindale Beck. There they occur in association with *Kjaerina geniculata* Bancroft, *Reuschella* sp. nov. and *Dolerorthis* sp. The figured specimens are from localities B. 5 and B. 6, but the same form has been found also at B. 10 (see Text-fig. 3). These are the only records of *Lonchodomas* from the Upper Longvillian of the Anglo-Welsh area.

HOLOTYPE. In. 49968 (Pl. 6, fig. 2).

PARATYPES. In. 49946 (Pl. 6, fig. 8); In. 49967 (Pl. 6, fig. 6).

DISCUSSION. The Swindale Beck species bears an obvious relationship to *Lonchodomas rostratus* (Sars) which has been refigured by Størmer (1940 : 128, pl. 2, figs. 1–4). The latter species has, however, a smaller proportion of the glabella projecting in front of the fixigenae, and the pygidium of the Norwegian form, the type-specimens of which were obtained from the Ampyx Limestone (zone of *Nemagraptus gracilis*) near Oslo, differs also in having only one pair of well-defined, distally situated, pleural furrows, which die out before attaining the axial furrows.

Lonchodomas politus (Raymond, 1925 : 39, pl. 2, figs. 8, 9; Cooper, 1953 : 18, pl. 6, figs. 1, 2, 5–10), from the " Upper Lenoir Limestone " of Black River age in Tennessee, has a conspicuously punctate test and a pygidium bearing seven or eight pairs of furrows, only the first of which is deeply impressed, but otherwise much resembles the Cross Fell species.

The stratigraphically younger species *Lonchodomas pennatus* (La Touche), discussed elsewhere in the present paper, has a relatively larger proportion of the glabella projecting in front of the fixigenae, whilst the pygidium has a less well-differentiated axis than that of *L. swindalensis*, and only one pair of pleural furrows.

Lonchodomas pennatus (La Touche)

(Pl. 6, figs. 1, 3–5, 9, 12)

1884. *Ampyx pennatus* La Touche, p. 57, pl. 3, fig. 56.
1891. *Ampyx tetragonus* Angelin : Nicholson & Marr, p. 511.
1932. *Ampyx* (*Lonchodomas*) *pennatus* La Touche : Reed, p. 205, pl. 11, figs. 5–7.
1949. *Lonchodomas pennatus* (La Touche) Bancroft, p. 299, pl. 10, fig. 17.
1958. *Lonchodomas pennatus* (La Touche) : Dean, pp. 213, 224.
1959*a*. *Lonchodomas pennatus* (La Touche) : Dean, pp. 200, 207.
1960. *Lonchodomas pennatus* (La Touche) : Dean, p. 82, pl. 11, figs. 2, 5, 8–12.

Several cranidia agreeing in all essentials with La Touche's species have been collected from the Dufton Shales. The often indifferent preservation renders precise measurement difficult, most of the specimens being compressed vertically, but the proportions are close to those of similarly preserved Shropshire material, the length of the cranidium, measured from the base of the frontal spine to the posterior margin of the occipital ring, being slightly more or less than three-quarters of the maximum breadth. A feature not previously seen in *L. pennatus* but now preserved in one specimen (Pl. 6, fig. 1) is the retroussé form of the prismatic frontal spine, which curves forwards and gently upwards from the glabella : a similar curvature is seen also in *Ampyx salteri* Hicks and *Ampyx linleyensis* (Whittard, 1955, pl. 1, fig. 17 ; pl. 2, fig. 6). A few individuals have traces of a slight median ridge or carina on the glabella, and this may be either accentuated by lateral compression or absent altogether. A similar ridge occurs in some Shropshire specimens, but its presence varies with the state of preservation. Two probably immature pygidia from Cross Fell (Pl. 6, fig. 5) are proportionately broader than the *forma typica*, their length : breadth radio being 1 : 3, but in mature pygidia this changes to about 1 : 2, that is to say, generally comparable with the Shropshire material.

HORIZON AND LOCALITIES. In the Knock-Dufton district *Lonchodomas pennatus* appears for the first time in the Onnian Stage, *Onnia gracilis* Zone, of Pus Gill, at localities A. 8, 9, 12 and 14. It has been found less commonly in the overlying *Onnia superba* Zone of Pus Gill, at localities A. 5 and 16. The ensuing Pusgillian Stage has yielded specimens at both Pus Gill, localities A. 6, 18 and 28, and Swindale Beck, locality B. 25.

DISCUSSION. La Touche's holotype was obtained from the Onnian Stage, *Onnia superba* Zone, in the Onny Valley of south Shropshire, in which district *Lonchodomas pennatus* ranges upwards from the Actonian Stage (Dean, 1960 : 83). The discoveries in the Pusgillian Stage of the Cross Fell Inlier increase the known vertical range of the species, but there is no information yet regarding its relationship to still younger forms, though there is a general resemblance to certain species of Ashgill age, for example that figured by Reed (1905 : 97, pl. 4, fig. 2) as *Ampyx* (*Lonchodomas*) cf. *rostratus* Sars from the Slade Beds of Haverfordwest.

Elsewhere, a small cranidium of *Lonchodomas* which may be conspecific with *L. pennatus* has been figured by Størmer (1945, pl. 2, fig. 10) as *Lonchodomas* aff. *rostratus* (Sars) from the *Tretaspis* Shales of Hadeland, a horizon approximately equivalent to the Pusgillian Stage. *Lonchodomas carinatus* (Cooper, 1953 : 17, pl. 7, figs. 12–17, 19–23) from the Black River Stage of Tennessee bears a strong resemblance to *L. pennatus* but possesses an irregularly punctate test, and the glabella projects less far forwards in front of the fixigenae. The pygidium of *L. carinatus* differs in having at least four discernible axial rings.

Family TRINUCLEIDAE Hawle & Corda, 1847

Subfamily CRYPTOLITHINAE Angelin, 1854

Genus ***BROEGGEROLITHUS*** Lamont, 1935

TYPE SPECIES. *Cryptolithus broeggeri* Bancroft, 1929 by original designation.

Broeggerolithus nicholsoni (Reed)

(Pl. 6, figs. 7, 11?, 14? ; Pl. 7, figs. 1–12)

1891. *Trinucleus goldfussi* Barrande ?, Nicholson & Marr, p. 509.
1891. *Trinucleus seticornis* Hisinger ?, Nicholson & Marr, p. 509.
1910. *Tinucleus nicholsoni* Reed, p. 212, pl. 16, figs. 1–9.
1912. *Trinucleus nicholsoni* Reed : Reed, pl. 18, fig. 6 ; pl. 19, figs. 4, 4*a*.
1914. *Trinucleus gibbifrons* M'Coy : Reed, p. 356, pl. 29, fig. 6.
1914. *Trinucleus nicholsoni* Reed : Reed, p. 357.
1927. *Cryptolithus nicholsoni* (Reed) Stetson, p. 88.
1940. *Broeggerolithus nicholsoni* (Reed) Whittington, p. 245.
1948. *Broeggerolithus nicholsoni* (Reed) : Bancroft *in* Lamont, p. 416.
1959*a* *Broeggerolithus nicholsoni* (Reed) : Dean, pp. 212, 214, 220.
1960. *Broeggerolithus* sp. (? nov.) Dean, p. 119, pl. 17, fig. 12.
1960. *Broeggerolithus simplex* Dean, p. 120, pl. 17, fig. 14.

DESCRIPTION. The cephalon is sub-semicircular in outline, broader than long, the maximum breadth of the syntypes ranging from 14 mm. to about 22 mm. The glabella is of moderate breadth, equal to about two-thirds of the total length, and often carries a small, apical ocellus just forward of centre. A pair of small, basal, glabellar furrows with apodemes is located immediately in front of a second pair of apodemes situated at the distal ends of the occipital furrow. The glabella is separated from the convex cheek-lobes by moderately-deep, almost straight, axial furrows. The occipital ring is small, strongly convex transversely, produced backwards and upwards to form a broadly-based occipital spine. The cephalic fringe is moderately declined, both frontally and laterally, though this may not always be apparent owing to compression of the specimen within a shaly matrix. The upper surface of the fringe is generally smooth and there is no development of raised interradial ridges such as are found in some earlier species of *Broeggerolithus*, for example *B. broeggeri* (Bancroft). One or two specimens show suggestions of such ridges, but these are almost certainly due to crushing and are not of constant form. There are four concentric rows of fringe-pits in front of the glabella, where the breadth (*sag.*) of the fringe contracts slightly so as to accommodate the frontal lobe of the glabella. There is a strong radial arrangement of pits frontally, and this persists laterally. The concentric arrangement is also marked, and the variation and norm of the four outer rows of pits is as follows : E_2 = 19–24 (22), E_1 = 21–23 (21), I_1 = 21–22 (22), I_2 = 20–22 (21). Up to three pits of E_2 may be missing at the genal angle, and in certain rare instances an occasional pit of E_2 may be absent laterally or anterolaterally. There is a notable lack of auxiliary E_2 pits such as are found laterally in certain related species of *Broeggerolithus*. There is little marked differentiation in the size of pits, but those of I_1 and I_2 are slightly larger than the others, especially towards the posterior margin of the fringe. E_2 and E_1 are sited close together, but E_1 and I_1 are separated by a smooth, narrow, concentric " band " corresponding in position with a conspicuous girder on the underside of the fringe. A similar band of equal breadth separates I_1 and I_2, marking the position of a second less well developed pseudo-girder. There are seven to nine, most commonly eight, pits along the posterior margin of the fringe. I_3 usually comprises fourteen or fifteen small pits, and is developed from R11 or thereabouts. The posterior margins of the fringe run slightly backwards, delimiting small genal prolongations, towards the genal angles which are produced to form librigenal spines ; the latter curve gently outwards and backwards, and their length is at least equal to that of the cephalon.

One of the syntypes, A. 29607, retains only five thoracic segments of typical trinucleid form. The axis of each is narrow (*tr.*) and bears a pair of apodemes situated just above the axial furrows. On each pleura, a moderately-deep pleural furrow, situated just forwards of centre, runs obliquely backwards from the axial furrow to the pleural point. A complete topotype thorax (Pl. 7, fig. 4) exhibits the customary complement of six thoracic segments.

The syntype pygidium, A. 29615 (Pl. 7, fig. 2), is preserved as an internal mould and few details can be seen. The axis has three clearly defined axial rings, and three or four more are less well defined. The pleural lobes have three, or perhaps four, segments, separated by faint pleural furrows and widening (*exsag.*) towards the lateral margins.

HORIZON AND LOCALITIES. All Reed's syntypes were described by him as having been collected solely from the Alston Road cutting near Melmerby, but the state of preservation of most of the specimens indicates that they came from what are known as the Lower Melmerby Beds, and the probable type-locality is believed to be that shown in the present paper as locality J (see Text-fig. 5). One syntype, Sedg. Mus. A. 29614, is preserved differently from the rest and the matrix suggests a probable origin in the Upper Longvillian strata such as are found at Alston Road, locality H. All the other localities, from A to G, along the Alston Road have yielded *Broeggerolithus nicholsoni*, but the specimens are, in general, smaller than the syntypes.

Although trinucleid trilobites are so abundant almost everywhere at the Alston Road outcrop, elsewhere in the Inlier they are almost unknown from strata of Longvillian age. An uncommon exception is locality E. 3 at Harthwaite Sike where rare fragments, referred to *B.* cf. *nicholsoni* (see Pl. 1, figs. 11, 14), occur with an assemblage indicating the *Bancroftina typa* Zone of the Lower Longvillian.

LECTOTYPE, here chosen. Sedg. Mus. A. 29613 (Pl. 7, figs. 6, 9).

PARATYPES. Sedg. Mus. A. 29607; A. 29608; A. 29609 (Pl. 7, figs. 1, 7); A. 29610 (Pl. 7, fig. 10); A. 29611 (Pl. 7, fig. 5); A. 29612 (Pl. 7, fig. 8); A. 29614 (Pl. 7, fig. 11); A. 29615 (Pl. 7, fig. 2).

DISCUSSION. In a recent account of trinucleid trilobites in south Shropshire (Dean, 1960 : 103) the species assigned to the genus *Broeggerolithus* were divided into three groups on the basis of small but significant differences in the structure of the cephalic fringe. *B. longiceps* (Bancroft) and *B. transiens* (Bancroft) were placed together in Group 3, whilst *B. simplex* Dean was placed doubtfully in Group 2. The last-named species is here regarded as a synonym of *B. nicholsoni* and may also be placed in Group 3. *B. simplex* was founded on a small cranidium from the Lower Longvillian of the Onny Valley and was at that time believed to be distinct. The pit count, however, falls within the limits of variation now established for *B. nicholsoni*, and additional material from Shropshire tends to confirm the identity of the two species

The fringe of *Broeggerolithus transiens* closely resembles that of the Melmerby species but its pit-count for the four outermost rows is noticeably smaller, and there are a few auxiliary pits situated anterolaterally in E_2. *Broeggerolithus longiceps* is remarkably similar to *B. nicholsoni*. The former species is, unfortunately, known from only a comparatively small population sample in south Shropshire, but as far as can be ascertained the pit-count falls within the limits of that for *B. nicholsoni*. Like *B. transiens*, however, *B. longiceps* generally possesses a few auxiliary pits in E_2, though situated posterolaterally, and these have not been found in *B. nicholsoni*. It is not known whether this is an invariable characteristic of *B. longiceps*, but if this should not prove to be the case then there is no other valid reason for regarding the species as distinct from *B. nicholsoni*. Certain well-preserved Shropshire specimens of *B. longiceps* have reticulate cheek-lobes, a feature not seen on any of the syntypes of *B. nicholsoni* but found on several specimens of the latter species from the Upper Melmerby Beds of the Alston Road cutting.

Outside the Cross Fell Inlier *Broeggerolithus nicholsoni* probably occurs at several localities in North Wales, associated with faunas of Longvillian age.

Broeggerolithus melmerbiensis sp. nov.

(Pl. 6, figs. 10, 13)

1959*a*. *Broeggerolithus* aff. *nicholsoni* (Reed) *pars*, Dean, p. 214.

DIAGNOSIS. Large *Broeggerolithus* generally similar to *B. nicholsoni* but with large number of fringe-pits, about one hundred, in four outermost concentric rows. Both E_1 and E_2 extend to the genal angles.

DESCRIPTION. One well-preserved specimen collected from the Alston Road cutting appears to resemble *Broeggerolithus nicholsoni* in most respects, but possesses a number of fringe-pits much larger than the norm for that species. The specimen has a closely similar radial and concentric arrangement of pits, but particularly noticeable is the manner in which rows E_2 and E_1 are placed close together, whilst rows E_1 and I_1 are separated from each other by a wide, concentric " band " which coincides with the girder on the underside of the fringe. I_1 and I_2 are similarly separated from each other, and the pits composing these two rows become larger in size towards the posterior margin of the fringe. A conspicuous feature is the way in which both E_1 and E_2 are developed as far as the genal angles. Both I_3 and I_4 consist essentially of pits which are comparatively small, though increasing slightly in size posteriorly, and the two rows are developed respectively from R13 and R19. The pit count for the specimen is as follows: E2 = 24 pits, E1 = 25 pits, I1 = 26 pits, I2 = about 25 pits. There are four continuous concentric rows of pits in front of the glabella, and seven pits are situated along each posterior margin of the fringe. The total number of pits in rows E2 to I2 inclusive is about one hundred, compared with an average of about eighty-five in *Broeggerolithus nicholsoni* (*s. s.*). The single available cranidium possesses four attached thoracic segments of typical *Broeggerolithus* aspect, but the total number originally present is unknown, as is the pygidium.

HORIZON AND LOCALITY. The holotype was collected from a loose nodule of impure limestone immediately below locality A in the Alston Road cutting, three-quarters of a mile north-east of Melmerby (see Text-fig. 5). It is almost certain that the specimen did, in fact, derive from this locality. The horizon is in the Longvillian Stage, and the strata at this point are believed to be the Upper Melmerby Beds, of Upper Longvillian age (Dean, 1959*a* : 213). The associated fauna includes *Broeggerolithus nicholsoni*, *Brongniartella* and *Flexicalymene*.

HOLOTYPE. BM. In. 52558.

DISCUSSION. Although bearing a general resemblance to certain other species of *Broeggerolithus* such as *B. nicholsoni*, *B. longiceps* and *B. transiens*, the new form is unlikely to be confused with them on account of its much higher pit-count for the four outer rows, whilst no other species exhibits a comparable development of E_2 to the genal angles.

***Broeggerolithus* cf. *transiens* (Bancroft)**

(Pl. 8, figs. 1, 3, 4, 6, 8, 11)

1929. *Cryptolithus transiens* Bancroft, p. 90, pl. 2, fig. 5.
1959*a*. *Broeggerolithus transiens* (Bancroft) Dean, pp. 196–8, 207.
1960. *Broeggerolithus transiens* (Bancroft): Dean, p. 123, pl. 18, figs. 2, 3, 7, 8, 11, 14. This reference contains a list of all other synonyms.

Numerous cephala and cranidia have been found, agreeing in all essentials with the description of the species from the type-area of south Shropshire (Dean, 1960 : 123). The pit count for the various rows of the cephalic fringe falls within the limits of variation of the Shropshire specimens, but instead of having one or two pits of E_1 marginal at the genal angle, the Cross Fell specimens commonly have three pits so situated, though the number has been found to vary from one to four. Generally there are up to two auxiliary pits in the outermost concentric row, E_2, of the Shropshire specimens, and these may sometimes be absent from the Cross Fell examples. This casts some doubt on the validity of such a feature as a means of separating closely-related species, but too few complete cranidia are available from either

Shropshire or Cross Fell to give reliable statistics for the variation in E_2. An analogous situation has already been noted with regard to *Broeggerolithus nicholsoni* and *B. longiceps*. The species is more abundant in the mudstones of the Cross Fell Inlier than in the corresponding coarser sediments of south Shropshire, and individuals frequently attain a larger size, the largest-known cephalon having a breadth of about 25 mm.

Horizon and localities. In the Knock-Dufton district *Broeggerolithus* cf. *transiens* is fairly common in Dufton Shales of the Marshbrookian Stage at Swindale Beck. There it occurs in small numbers in strata thought to belong to the middle portion of the stage (locality B 12), but becomes more abundant in higher strata (localities B. 11, 14, 16) which contain *Kjerulfina* cf. *polycyma* Bancroft and are considered to be equivalent to the *Onniella reuschi* Zone of south Shropshire. *B.* cf. *transiens* occurs also in Harthwaite Sike, east-south-east of Dufton (see Text-fig. 4) at localities E. 7, 8, 9?, 10–12, but the fauna there is sparse, composed in the main of smaller individuals.

Broeggerolithus sp.

(Pl. 8, fig. 2)

1959*a*. *Broeggerolithus* sp. (pars.) Dean, p. 207.

Among the numerous trinucleid trilobites found in the Marshbrookian rocks of Swindale Beck is one individual quite different from all the rest. The specimen comprises a fragmentary cranidium preserved as a limonitic external mould in a dark-grey, cleaved mudstone. The estimated length and breadth of the original cephalon are respectively 12 mm. (approx.) and 26 mm. Its most distinctive feature is the manner in which the two outermost concentric rows of pits, E_2 and E_1, end abruptly without extending to, or even near, the genal angle as is customary in normal forms of *Broeggerolithus*. E_2 extends only to the anterolateral angle, leaving three pits of E_1 external to the margin. E_1 stops far short of the genal angle, leaving five pits of I_1 external to the margin, though separated from it by a smooth band which is equal in breadth to one row of pits. Such an arrangement results in the somewhat unusual, indented form of the cephalic margin in front of the genal angle, and the obliquely truncated shape of the anterolateral angle. The estimated number of pits originally present is as follows: $E_2 + e_2 = 12$, $E_1 + e_1 = 15$, $I_1 + i_1 = 19$, $I_2 + i_2 = 19$, $I_3 + i_3 = 10$. There is a small triangular group of eight pits situated between I_2 and I_3 near the posterior margin of the fringe, and seven pits are aligned parallel to the latter. The pits of E_1 and I_{1-2} are of roughly equal size, larger than those of E_2 and I_3. The last four pits of I_2 nearest the posterior margin are of particularly large size.

Horizon and locality. Found in mudstones of the Dufton Shales which contain *Broeggerolithus* cf. *transiens* (Bancroft) and *Kjerulfina* cf. *polycyma* (Bancroft), and belong to the topmost part of the Marshbrookian Stage, at locality B. 16 in Swindale Beck.

Discussion. It is not unusual for specimens of *Broeggerolithus* to have a deficiency in the number of E_2 pits near the genal angle, and in such forms as *B.*

soudleyensis (Bancroft) and *B. globiceps* (Bancroft) some E_2 pits may be absent frontally, but no known species compares in any way with the excessive loss of pits in the specimen now figured. In view of the large number of specimens of normal *Broeggerolithus* cf. *transiens* associated with the cranidium it seems likely that the specimen represents a rare mutation or pathological form. Consequently it is not proposed to erect a new specific name, at least until further material is available.

Genus *ONNIA* Bancroft, 1933

TYPE SPECIES. *Cryptolithus superbus* Bancroft, 1929 by original designation of Bancroft (1933 : 2).

Onnia gracilis (Bancroft)

(Pl. 8, figs. 12, 13)

1929. *Cryptolithus gracilis* Bancroft, p. 94, pl. 2, figs. 8, 9.
1959*a*. *Onnia gracilis* (Bancroft) Dean, p. 207.
1960. *Onnia gracilis* (Bancroft) : Dean, p. 130, pl. 19, figs. 2, 7. This reference contains a comprehensive synonymy of the species.

This species has recently been redescribed in detail by the writer (Dean, 1960 : 130) who gave the following figures for the range in variation of the number of pits present in the outermost four rows of the fringe. $E_2 + e_2 = 31–37$ (34), $E_1 + e_1 = 21–25$ (22), $I_1 + i_1 = 21–25$ (23), $I_2 + i_2 = 21–25$ (23) The figure in brackets represents the mode. Insufficient well-preserved material is available from the Cross Fell Inlier to give authentic figures for the corresponding variation, but the available material has yielded the following results: $E_2 + e_2 = 32–37$, $E_1 + e_1 = 20–23$, $I_1 + i_1 = 20–22$, $I_2 + i_2 = 21–22$. It is therefore apparent that the specimens fall within, or are very close to, the permissible variation for the species in its type-area.

HORIZON AND LOCALITIES. As in south Shropshire *Onnia gracilis* characterizes the middle portion of the Onnian Stage. It has been found in some abundance in black mudstones of the Dufton Shales at Pus Gill, localities A. 8, 9, 11, 12, 13, 14 and 15. Again, as in Shropshire, the species is accompanied by a fauna which includes *Onnicalymene onniensis* (Shirley), *Lonchodomas pennatus* (La Touche), *Chonetoidea* sp. and *Onniella broeggeri* Bancroft.

Onnia superba (Bancroft) ***pusgillensis*** Dean

(Pl. 8, figs. 5, 7, 9, 10)

1961. *Onnia superba pusgillensis* Dean, p. 120, pl. 7, figs. 1–6. Includes full synonymy.

Onnia superba (Bancroft), the zone fossil of the topmost subdivision of the Onnian Stage in south Shropshire, has not been found in the Cross Fell Inlier, but is thought to be represented by a distinct, and possibly local, subspecies *O. superba pusgillensis*. Although resembling *O. superba* in almost all respects the Cross Fell form may easily be distinguished by the continuous development of I_2 in front of the glabella, and by the greater development of I_3 and I_4, respectively from R3 or R4, and R7.

HOLOTYPE. BM. In. 55707.

PARATYPES. BM. In. 50005 (Pl. 8, fig. 9) ; In. 50008 (Pl. 8, fig. 5) ; In. 50049 ; In. 55704 ; In. 55705 ; In. 55706 ; In. 55708.

HORIZON AND LOCALITIES. Dufton Shales, Onnian Stage, *Onnia superba* Zone, Pus Gill, localities A. 5 and A. 16.

Subfamily TRETASPIDINAE Whittington, 1941

Genus ***TRETASPIS*** M'Coy, 1849

TYPE SPECIES. *Asaphus seticornis* Hisinger, 1840 by subsequent designation of Bassler (1915 : 1285).

Tretaspis cf. ***ceriodes*** (Angelin) ***donsi*** Størmer

(Pl. 10, figs. 4, 6, 8)

1945. *Tretaspis ceriodes* (Angelin) var. *donsi* Størmer, p. 405, pl. 1, fig. 8.
1959*a*. *Tretaspis* cf. *ceriodes* (Angelin) : Dean, p. 207.
1961. *Tretaspis* cf. *ceriodes donsi* Størmer : Dean, p. 129, pl. 9, figs. 7–9.

In southern Norway, *Tretaspis ceriodes donsi* has been shown by Størmer (1945 : 404) to be restricted to the upper part of the Upper Chasmops Limestone, 4bδ. The earliest-known occurrence of *Tretaspis* in the Cross Fell Inlier is at Pus Gill, locality A. 13, in Dufton Shales belonging to the *Onnia gracilis* Zone of the Onnian Stage, and the evidence at this point, though fragmentary, suggests a comparison with the Norwegian subspecies. Additional, better-preserved material from the *Onnia superba* Zone at Pus Gill, locality A. 5, is too incomplete for detailed comparison, but shows all the principal features of *T. ceriodes donsi*. The horizon of the Cross Fell specimens corresponds fairly closely with that of the Norwegian material.

Tretaspis convergens Dean

(Pl. 10, figs. 1, 3, 5)

1961. *Tretaspis convergens* Dean, p. 127, pl. 9, figs. 1–6.

A detailed description of this species has already been given (Dean, 1961 : 127) to which nothing need be added here. *T. convergens* is a distinctive form, its closest relationships being with the species-group typified by *Tretaspis seticornis* (Hisinger), particularly *T. seticornis* var. *anderssoni* Størmer (1945 : 402, pl. 1, fig. 2). *T. convergens* has so far been found at only one locality in the Cross Fell Inlier, namely B. 25 in Swindale Beck. There it occurs in the highest part of the Dufton Shales, belonging to the Pusgillian Stage, so that it is generally contemporaneous with *Tretaspis seticornis anderssoni* and allied forms as found in Etage 4cα of southern Norway.

HOLOTYPE. BM. In. 50059*a*, *b* (Pl. 10, figs. 1, 3, 5).

Paratypes. In. 50030 ; In. 50037 (Pl. 10, fig. 2) ; In. 50058*a*, *b*.

Tretaspis kiaeri Størmer ***radialis*** Lamont

(Pl. 9, figs. 2–4)

1941. *Tretaspis kjaeri* mut. *radialis* Lamont, 1941, p. 456, figs. 5, 6.
1961. *Tretaspis kiaeri radialis* Lamont: Dean, p. 122, pl. 7, figs. 7–9, pl. 8, figs. 1, 3–5. Includes full synonymy of the subspecies.

The majority of the abundant specimens of *Tretaspis* collected from the Dufton Shales of the Cross Fell Inlier can be referred to this subspecies. *T. kiaeri radialis* was founded originally on two fragmentary specimens from the Portrane Limestone of Eire, but the description has since been supplemented, using material from the Dufton Shales (Dean, *loc. cit.*), and the affinities with other species discussed.

HORIZON AND LOCALITIES. All the known specimens are from Dufton Shales belonging to the Pusgillian Stage. The exact distribution within the Pusgillian is not clear, owing to the predominance of successions affected by strike-faulting, but the subspecies appears to occur throughout most of the stage. Localities include the following: Pus Gill, A. 6, A. 18, A. 21, A. 24 to A. 30; Swindale Beck, B. 18, B. 22 to B. 26, B. 28, B. 33, B. 34; Dufton Town Sike, C. 1 to C. 6; Billy's Beck, D. 1; also the section at Hurning Lane, one mile north of Dufton.

Tretaspis kiaeri Størmer ***duftonensis*** Dean

(Pl. 9, figs. 1, 5–7)

1961. *Tretaspis kiaeri duftonensis* Dean, p. 125, pl. 8, figs. 2, 6–8.

The subspecies was described from a single, well-preserved specimen collected from Dufton Shales belonging to the Pusgillian Stage at Pus Gill, locality A. 27. Its closest relationship would appear to be with *T. kiaeri radialis*, from which it differs in having a conspicuously larger pit-count for E_{1-2}, a less well-developed concentric arrangement of I_{2-4} posterolaterally, as well as a larger, triangular area of irregularly arranged pits on the genal prolongations of the fringe. *T. kiaeri duftonensis* is not known with certainty outside the type-locality, though fragments of fringe suggest that it may occur elsewhere at Pus Gill, but identification is difficult in the absence of better-preserved material.

HOLOTYPE. BM. In. 50020a, b.

Family CHEIRURIDAE Salter, 1864

Subfamily CYRTOMETOPINAE Öpik, 1937

Genus ***PSEUDOSPHAEREXOCHUS*** Schmidt, 1881

TYPE SPECIES. *Sphaerexochus hemicranium* Kutorga, 1854 by subsequent designation of Reed (1896*a*: 119).

Pseudosphaerexochus cf. *octolobatus* (M'Coy)

(Pl. 10, figs. 7, 9–12)

?1891. *Youngia trispinosa* Nicholson & Etheridge : Nicholson & Marr, p. 511.
1959*a* *Pseudosphaerexochus* sp. nov., Dean, pp. 204, 208.

DESCRIPTION. The cephalon is known only from the cranidium. The glabella is strongly convex both longitudinally and transversely, subovate in plan, its maximum breadth about, or slightly greater than, three-quarters of the sagittal length. It is bounded by deep, evenly-curved axial furrows, strongly convex abaxially, with deep, hypostomal pits. The frontal lobe is small, rather less than one-quarter of the glabellar length, and there are three pairs of equispaced glabellar furrows. The first and second pairs are parallel, extending inwards about one-quarter of the glabellar breadth ; they intersect the axial furrows at right-angles, but curve thence adaxially backwards, at the same time becoming rapidly shallower. The first and second pairs of glabellar lobes are identical in size and form, their convexity in line with the remainder of the glabella. The third glabellar furrows are deeper than, and parallel to, the first and second pairs, but curve backwards without reaching the occipital furrow and become shallower proximally. The occipital ring is small, narrow (*tr.*), strongly convex transversely, separated from the glabella by a moderately deep occipital furrow. The fixigenae are small, convex, and steeply declined abaxially. The pleuroccipital segment becomes slightly longer (*exsag.*) laterally, ending posterolaterally in a pair of short, broad, blunt fixigenal spines set a short distance inwards from the lateral margins. The pleuroccipital furrow is transversely straight for the most part, becoming shallower distally where it curves forwards towards, though without reaching, the lateral margins. The eyes have not been found preserved. The palpebral lobes are narrow, moderately convex abaxially, strongly arched longitudinally, and slightly divergent backwards ; they are defined proximally by palpebral furrows of moderate depth which die out quickly to both front and back. The anterior branches of the facial suture extend forwards from the eyes, parallel to the axial furrows, to cut the anterior border, whilst the posterior branches curve backwards distally to intersect the lateral margins just in front of the line of the pleuroccipital furrow. The librigenae have not been found. The surface of the glabella is covered with fine, evenly distributed granules, whilst all the furrows are smooth. The surface of the fixigenae is covered with large, dispersed pits, the intervening spaces, together with the surface of the pleuroccipital segment, being covered with smaller punctae which are apparent only on the external mould. The internal mould of the glabella is ornamented with closely-grouped, small, prickly granules, probably representing the infillings of canals in the original test.

The hypostoma and thorax are not known.

An incomplete pygidium, which must have been more than twice as broad as long, is the only specimen that has been found (Pl. 10, fig. 7). It is made up of four segments which are produced backwards to form four pairs of strong, tapering spines ; the latter are separated from one another by well-defined notches, and their tips are stepped backwards slightly *en echelon* from first to fourth. Only three axial segments are visible, the first two well defined by deep ring furrows, and the third poorly defined by two shallow transverse notches near the bases of the fourth pair of pleural spines. The axial furrows comprise broad, shallow grooves, moderately convergent backwards. Excluding the furrows, the surface of the pygidium is granulate on the internal mould, but finely pitted on the external mould.

Horizon and localities. The earliest-known occurrence of the species in the Cross Fell Inlier is in the Dufton Shales, Onnian Stage, *Onnia superba* Zone of Pus Gill, locality A. 5. Most of the available specimens are, however, from Dufton Shales belonging to the Pusgillian Stage at Swindale Beck, locality B. 25. Other localities, all in Pusgillian strata, are at Pus Gill, localities A. 6 and A. 30, and at Dufton Town Sike, locality C. 6, east of Dufton.

Discussion. The specific name *Pseudosphaerexochus octolobatus* has been used to cover forms of the genus occurring in British Ordovician strata of various ages. The holotype, described and figured by M'Coy (1849 : 407 ; *in* Sedgwick & M'Coy, 1851, pl. 1G, fig. 10) as *Ceraurus octolobatus*, is a pygidium, Sedg. Mus. A. 11606, from the Rhiwlas Limestone, of Ashgill age, near Bala, and the species must be redescribed in detail before satisfactory comparisons can be made. Specimens from the Ashgill Series, Drummuck Group, of Girvan were assigned by Reed (1906 : 141, pl. 18, figs. 8–11) to *Cheirurus* (*Cyrtometopus*) *octolobatus*, and these appear to be identical with the Cross Fell specimens, at least as far as the cephalon is concerned.

Pseudosphaerexochus has been recorded from the Onnian Stage of the Onny Valley in south Shropshire (Dean, 1961*a* : 316), but the material there is too fragmentary for comparison with that from Cross Fell.

Family Encrinuridae Angelin, 1854

Subfamily Encrinurinae Angelin, 1854

Genus ***ENCRINURUS*** Emmrich, 1844

Type species. *Entomostracites punctatus* Wahlenberg, 1821 by original designation of Emmrich (1844 : 16).

Encrinurus sp.

(Pl. 11, figs. 1, 4)

1959*a*. *Encrinurus* sp., Dean, p. 214.

Only one specimen has been collected, a pygidium about 5 mm. long and 4·5 mm. broad frontally, preserved as an internal mould with part of the corresponding external mould. Frontally the axis occupies about one-quarter of the maximum breadth ; it is delimited by deep, smooth axial furrows and tapers backwards to a narrow tip. There are eight pairs of pleural ribs which terminate laterally in small free points ; the pleurae of the eighth pair almost coalesce with the terminal piece of the axis, from which they are separated by a pair of shallow grooves. The axis as far as the eighth pair of pleurae carries fifteen axial rings, but beyond this position is apparently smooth. The ring furrows, apart from the first three or four, become shallower medially and there are traces of small median nodes on the third, fifth and eighth axial rings. The remainder of the dorsal surface is smooth.

HORIZON AND LOCALITY. Locality H (see Text-fig. 5) beside the Alston Road, three-quarters of a mile north-east of Melmerby. The strata, the Upper Melmerby Beds, contain fossils indicating the lower part of the Upper Longvillian Substage, the equivalent of the *Kjaerina bipartita* Zone or Alternata Limestone in south Shropshire.

DISCUSSION. Few Caradoc species of *Encrinurus* are available for comparison. *Encrinurus* sp. (? nov.) from the Marshbrookian Stage of Shropshire (Dean, 1961*a*, pl. 49, figs. 10, 12) has a similar number of ribs but a larger number of axial rings, at least seventeen. The Alston Road specimen may well prove to represent a new species.

Subfamily DINDYMENINAE Přibyl, 1953

Genus ***DINDYMENE*** Hawle & Corda, 1847

TYPE SPECIES. *Dindymene fridericiaugusti* Hawle & Corde, 1847 by subsequent designation of Barrande (1852 : 816).

Dindymene duftonensis sp. nov.

(Pl. 11, fig. 13)

1959*a*. *Dindymene* sp. nov., Dean, pp. 198, 207.

The holotype is an incomplete cranidium of estimated breadth 4 to 5 mm., excluding fixigenal spines, the maximum breadth being roughly twice the length. The glabella is strongly convex, both longitudinally and transversely, narrow posteriorly but expanding forwards until equal to rather more than one-third of the cephalic breadth. The axial furrows are deep and narrow posteriorly, but widen forwards where they curve distally to join the lateral border furrow which skirts the plump fixigenae. The occipital furrow is shallow and broad (*sag.*) medially, deepening laterally where a pair of deep apodemal pits is situated ; the occipital ring is small, curving forwards abaxially to form a pair of occipital lobes. The pleuroccipital segment is uniformly narrow (*exsag.*), transversely straight, separated from the fixigenae by a parallel, moderately-deep, pleuroccipital furrow. The external mould shows that the narrow (*tr.*) lateral borders meet the pleuroccipital segment at the genal angles which are produced to form a pair of fixigenal spines, long, slender, slightly curved, convex side forwards, and broadly splayed backwards. The surface of the fixigenal spines, lateral border and pleuroccipital segment is uniformly and finely granulate, appearing almost smooth. The surface of each fixigena is covered with fine wrinkles, which contain numerous small pits, and carries seven large tubercles ; three of the latter are situated anterolaterally in a row parallel to the lateral border furrow, one is situated medially just in front of the pleuroccipital furrow, and the remainder are arranged more or less sporadically over the fixigena. The surface of the glabella, though incomplete, is estimated to have carried about twenty tubercles of moderate size. Three of these form a median, longitudinal row extending half-way from the occipital furrow to the front of the glabella and are flanked by two pairs of tubercles situated a short distance adaxially from the axial furrows. The remaining tubercles are grouped more closely together across the frontal lobe, and the intermediate spaces are finely granulate. These figures apply to the partially preserved holotype, and the material available is insufficient to decide whether there is any variation in the disposition of the tubercles.

The remainder of the exoskeleton is unknown.

HORIZON AND LOCALITY. Dufton Shales belonging to the Marshbrookian Stage, probably the middle or upper third, at locality E. 12 (see Text-fig. 4) in Harthwaite Sike, east-south-east of Dufton.

HOLOTYPE. BM. In. 54652*a*, *b*, the latter, an external mould, being figured here in the form of a latex cast.

DISCUSSION. The known species of *Dindymene* were reviewed recently by Kielan (1959 : 146 *et seq.*). Of them, the species with which *D. duftonensis* may best be grouped are *D. ornata* Linnarsson, of Ashgill age, and *D. plasi* (Kielan, 1959 : 151, pl. 29, figs. 1–3) from the Llanvirn Series of Bohemia. Like them it is equipped with genal spines directed posterolaterally, but those of the Cross Fell species are notably longer. Both the extra-British species differ from *D. duftonensis* in having a particularly large tubercle, almost a cephalic spine, sited medially, one-third of the distance from the occipital furrow to the front of the glabella ; in this respect they somewhat resemble the more extreme development of a cephalic spine seen in the recently described *Cornovica*, from the Lower Llanvirn of west Shropshire (Whittard, 1960 : 122), a genus which possesses, however, glabellar furrows and eleven thoracic segments. The fixigenae of *D. duftonensis* carry a similar number of large tubercles to those of *D. plasi* and *D. ornata* : the glabella, however, has a greater number of tubercles than that of *D. ornata* but fewer than that of *D. plasi*. As with *D. ornata* the space between the glabellar tubercles is finely granulate, a feature apparently not found in *D. plasi*.

Harper's (1956 : 389) record of *Dindymene* cf. *ornata* from Upper Longvillian strata at Llanystwmdwy, Carnarvonshire, suggests that *D. duftonensis* may possibly be represented in the North Welsh faunas.

Dindymene **sp.**

(Pl. 11, fig. 6)

1959*a*. *Dindymene* sp., Dean, pp. 194, 207.

Two fragmentary cranidia, one of which is figured here, have been collected from the Upper Longvillian of Swindale Beck. In size and general form they match the type material of *D. duftonensis* but, as the dorsal surface is not preserved, precise identification has not been possible, though there are faint traces of some large tubercles. The more complete specimen has a narrow (*sag.*), upturned, anterior border, apparently separated from the glabella by a narrow (*sag.*), anterior border furrow containing the facial suture. The latter follows the outline of the frontal lobe as far as the axial furrow, beyond which it runs parallel to the margin of the cephalon and separates a narrow (*tr.*), smooth border from the fixigena. It has not been possible to trace the line of the suture beyond the anterolateral portion of the glabella.

HORIZON AND LOCALITY. Dufton Shales containing *Kjaerina geniculata* Bancroft and forming the upper part, the *Kjaerina typa* Zone, of the Upper Longvillian Substage, at locality B. 5 in Swindale Beck.

Subfamily CYBELINAE Holliday, 1942

Genus ***ATRACTOPYGE*** Hawle & Corda, 1847

TYPE SPECIES *Calymene verrucosa* Dalman, 1826 by original designation of Hawle & Corda (1847 : 90).

Atractopyge scabra sp. nov.

(Pl. 11, figs. 2, 3, 10)

1891. *Cybele verrucosa* Dalman : Nicholson & Marr, pp. 505, 511.
1959*a*. *Atractopyge* aff. *aspera* (Linnarsson) : Dean, p. 207.

DIAGNOSIS. Glabella clavate, slightly broader than long, with frontal lobe strongly convex forwards. Three pairs equisized glabellar lobes. Eye-ridges run from palpebral lobes towards first glabellar furrows. Surface of test, excluding furrows, covered with coarse tubercles, some of conspicuously large size. Pygidium longer than broad. Four pairs of ribs ending in free points arranged *en echelon*. Narrow axis with four continuous axial rings and a further fifteen or sixteen incomplete rings.

DESCRIPTION. The length of the cranidium is rather more than half the breadth. The glabella is moderately convex, clavate in outline, and attains its maximum breadth, slightly greater than the median length, across the lateral extremities of the anterior border. There are three pairs of glabellar furrows, represented by deep, almost slot-like pits situated a short distance adaxially from the axial furrows. The first pair of glabellar furrows is situated about mid-way between the frontal margin and the occipital furrow, the second and third pairs being then positioned at regular intervals so as to give three pairs of almost equisized glabellar lobes, their long axes strongly divergent forwards. The occipital ring is short (*sag.*), convex forwards medially ; laterally it curves forwards slightly to form a pair of occipital lobes, immediately in front of which a pair of apodemal pits is situated at the extremities of the broad (*sag.*), smooth, moderately-deep occipital furrow. The axial furrows are deep, wide (*tr.*), smooth, and rounded basally in cross-section ; from the occipital ring they follow a slightly divergent course forwards as far as the first glabellar furrows, whence they diverge more sharply to the false preglabellar field. The frontal lobe of the glabella is strongly convex forwards where it is bounded by a broad (*sag.*), smooth furrow, well defined but not deep, which intersects the axial furrows opposite a pair of deep, hypostomal pits. Beyond this furrow the anterior border is only slightly raised, but it is rendered more conspicuous by the presence thereon of a row of well-developed tubercles of both large and medium size. Ornamentation of similar type, but including a greater number of large tubercles, covers the surface of the remainder of the glabella with the exception of the glabellar lobes. In some individuals two, or even four, of the largest tubercles on the anterior border may be arranged symmetrically about the sagittal line, and two or three pairs of those on the main body of the glabella have been found to behave similarly, but it has not proved possible to utilize satisfactorily, with the available material, the notation proposed by Tripp (1957) for the tuberculation of certain species of *Encrinurus*. The fixigenae are strongly convex, with faint suggestions of eye ridges running towards the first glabellar furrows, and are surmounted by prominent, pedunculate, palpebral lobes. No palpebral furrows have been seen on the latter, which have a finely granulate, almost smooth surface, contrasting with the coarse tuberculation of the fixigenae which ends abruptly at the base of the palpebral lobes. The pleuroccipital furrow is straight for about half its length (*tr.*) but then turns markedly backwards and finally dies out just before reaching the lateral margins. The pleuroccipital segment, which follows the course of the pleuroccipital furrow, is extremely narrow (*exsag.*) near the axial furrows but then widens appreciably towards the apparently rounded genal angles. Each half of the pleuroccipital segment carries about seven or eight tubercles arranged fairly regularly along its length (*tr.*).

The librigenae, hypostoma and thorax are not known.

Only a few isolated pygidia have been found, the largest of which is just over 12 mm. long. The best-preserved specimen (Pl. 11, fig. 10) is about 9·5 mm. in length, with a maximum breadth of 8 mm. It is subovate in plan and only moderately convex transversely. There are four pairs of pleural ribs, separated from each other by strong rib furrows which become less well developed from first to fourth. The ribs of the first pair curve abaxially backwards for about half the length of the pygidium and then, more gradually, adaxially. The remaining ribs are subparallel to the first pair but become successively less strongly curved until those of the fourth pair are almost straight, converging backwards subparallel to the axial furrows. The ribs terminate in small, free points which are " stepped " backwards *en echelon* from first to fourth. The axis is in the form of an acute isosceles triangle, the two long sides of which meet posteriorly at about 20 degrees, and there may be up to nineteen, or perhaps twenty, axial rings visible. The first four axial rings are well defined, continuous with the corresponding pairs of ribs. Frontally the axial furrows are present merely as shallow grooves, but they become sharply defined behind the fourth axial ring. Sometimes a fifth axial ring may be defined by a transversely continuous ring furrow, but usually the greater part of the axis bears a smooth median band, occupying about one-third of its breadth, on either side of which the axial rings are clearly defined. There is a small, pointed terminal piece, behind which the points of the fourth pair of ribs extend a little way. The greater part of the surface of the pygidium is smooth but there are traces of incipient tubercles on occasional axial rings, whilst up to five larger tubercles may be found along each rib, particularly its hindmost two-thirds.

HORIZONS AND LOCALITIES. The earliest-known occurrences of *Atractopyge scabra* within the Cross Fell Inlier are in Dufton Shales belonging to the Onnian Stage at Pus Gill, where the species is uncommon in both the *Onnia gracilis* Zone, locality A 14, and the *Onnia superba* Zone, locality A 5. The new species is more common in the Pusgillian Stage, at which horizon it is known from Pus Gill, localities A. 25, 27 and 28; Swindale Beck, locality B. 25; and Dufton Town Sike, localities C. 2, 3 and 5.

HOLOTYPE. BM. In. 50154 (Pl. 11, fig. 2).

PARATYPES. BM. In. 50147; In. 50150 (Pl. 11, fig. 3); In. 50157 (Pl. 11, fig. 10).

DISCUSSION. The name " *Cybele verrucosa* Dalman ", a species described originally from the Red Tretaspis Shales of Västergötland, Sweden, has often been used in old faunal lists and collections from the Cross Fell Inlier, and from horizons of various ages elsewhere. This trilobite, the type species of *Atractopyge*, has recently been refigured by Henningsmoen (*in* Moore, 1959, fig. 349, 1*a*, *b*) whose illustrations show that it differs markedly from *A. scabra* in having a glabella which is less expanded frontally, with a smaller frontal glabellar lobe, as well as a pygidium which is proportionately shorter, carrying noticeably fewer (15) axial rings, and with the tips of the pleural ribs ending in line posteriorly.

The holotype of *Atractopyge michelli* (Reed, 1914*a*: 42, pl. 7, figs. 7, 7*a*–*c*) from the Balclatchie Group of Girvan is generally similar to *A. scabra*, but the glabella is less expanded frontally and more coarsely tuberculate, whilst the pygidium is proportionately shorter with fewer, less well-defined axial rings. *Atractopyge scabra* bears a strong resemblance to several forms of the genus said to have been collected from Ashgill strata in the Anglo-Welsh area, but until these have been investigated further it is impossible to say whether the species ranges higher than the Caradoc Series.

The lectotype pygidium of *Atractopyge atractopyge* (M'Coy *in* Sedgwick & M'Coy, 1851, pl. 1G, fig. 4 only; Dean, 1961*a*: 319), from the Caradoc Series, probably Longvillian Stage, of North Wales, is proportionately broader than that of *A. scabra* and has a less strongly tapered axis, probably with fewer and better-defined axial rings. M'Coy's illustration shows the pleural ribs ending in-line posteriorly, but this is not clear on the actual specimen.

Atractopyge? sp.

(Pl. 11, figs. 5, 8)

1959*a*. *Atractopyge* sp. ind., Dean, p. 214.

A single specimen, a fragmentary cranidium, from the Lower Melmerby Beds, Lower Longvillian Substage, at Alston Road, locality J, figured here in the form of a latex cast, shows features suggestive of *Atractopyge*. The glabella is incomplete but expands forwards and possesses three, almost equisized, pairs of glabellar lobes. The fixigenae stand as high as the glabella, decline steeply towards the axial furrows, and are topped by traces of pedunculate palpebral lobes. The surface of the test is covered with large granules interspersed with larger tubercles, some of which are arranged in pairs symmetrically about the sagittal line. The cranidium is too poorly preserved for comparison with known species, but forms an interesting addition to the trilobites known from the Longvillian Stage of the Anglo-Welsh area. A further specimen (Pl. 11, fig. 5), in a still worse state of preservation, from the Corona Beds, Lower Longvillian Substage, *Bancroftina typa* Zone, at

Harthwaite Sike, locality A. 3, shows only part of a glabella and occipital ring, together with part of the corresponding left fixigena and palpebral lobe. Generic determination is not possible and the specimen is figured here merely as *Atractopyge*? sp., but it may prove to be related to the Alston Road trilobite.

Genus ***PARACYBELOIDES*** Hupé, 1955

TYPE SPECIES. *Cybele loveni* Linnarsson var. *girvanensis* Reed, 1906 by original designation of Hupé (1955 : 271).

Paracybeloides cf. ***girvanensis*** (Reed)

(Pl. 11, figs. 7, 9, 12, 14, 15)

1891. *Cybele Loveni* Linnarsson : Nicholson & Marr, p. 511.
1906. *Cybele loveni* var. *girvanensis* Reed, p. 126, pl. 17, figs. 1–4.
1959*a*. *Paracybeloides* aff. *loveni* (Linnarsson) : Dean, pp. 207, 208.

Numerous specimens of *Paracybeloides* have been collected from the Dufton Shales, and agree in all essential respects with the type material described by Reed (*loc. cit.*) from the Ashgill Series of Girvan. According to Reed's original description the pygidial axis carries twenty-two to twenty-eight axial rings, but examination of several specimens, including syntypes, in the Gray Collection at the British Museum (Nat. Hist.) suggests that the average number of rings present is about twenty-three, whilst specimens with twenty or twenty-one rings are not unknown. The variation in the number of axial rings found on the Cross Fell specimens is from twenty to twenty-three, the most common number being twenty-one, and this slight difference is not considered here to be of sufficient importance for specific differentiation.

The tip of the pygidium of *P. girvanensis* was inaccurately illustrated by Reed (*loc. cit.*), who has been followed by other workers, for example Hupé (1955 : 272) and Henningsmoen (*in* Moore, 1959, fig. 349, 5*b*). Reed's illustration shows the terminal piece of the pygidial axis ending in front of the hindmost pair of pleural points which, according to him, were separated from each other by a small gap. In fact, the specimens figured by him, including BM. In. 23243 (Reed, 1906, pl. 17, fig. 4), possess a terminal piece which is produced postaxially into a long, flattened, pointed process, constituting the longest (*sag.*) portion of the pygidium and united abaxially with the proximal pair of pleural points so as to form a flattened, trifid, pygidial termination. One of the Cross Fell specimens, BM. In. 50178, shows that the terminal process described above was sometimes produced to an even greater degree, giving a slender, pointed spine ; the total length of this particular pygidium is approximately 17 mm., of which the axis *sensu stricto* occupies only about 10 mm.

Reed's illustrations of the cephalon of *P. girvanensis* show also that it possesses a smooth occipital ring. This is apparently the case in the syntypes, and also in other specimens, when preserved as internal moulds, but it is clear from the corresponding external moulds that they, together with the Cross Fell specimens, have a large median tubercle which may occasionally be produced backwards and upwards to form a blunt, occipital spine.

HORIZON AND LOCALITIES. *Paracybeloides* cf. *girvanensis* appears uncommonly in the Onnian Stage, *Onnia gracilis* Zone, of Pus Gill, locality A.5, but has not yet been recorded from the overlying *Onnia superba* Zone ; this apparent absence may be due to the paucity of exposures of the relevant strata. In the Pusgillian Stage the same species becomes more abundant and has been found at Pus Gill, localities A. 18, 25, 28–30 ; Swindale Beck, locality B. 25 ; and Dufton Town Sike, locality C. 2.

Paracybeloides sp.

(Pl. 11, fig. 11)

1959*a*. *Paracybeloides* sp. ind., Dean, p. 214.

One specimen only has been found in the Longvillian Stage, constituting the sole record of the genus at this horizon in the Anglo-Welsh area. It comprises a pygidium which, excluding spines, is about 5 mm. in length with a frontal breadth of about 4 mm. The axis is narrow, less than one-third the frontal breadth, and carries an estimated eighteen axial rings. Although the specimen is damaged, most of the axial rings can be seen to be obsolete medially, where a median band extends backwards from at least the fourth ring. The main body of the axis is relatively short, just over two-thirds of the total length of the specimen, but the terminal piece is long, slender, and produced backwards, though the tip is not visible. The pleural lobes are imperfectly preserved but appear to be of generally similar form to those of *Paracybeloides girvanensis*. The specimen is inadequate for detailed comparison with other species, but appears to be smaller and more slender than the pygidium of *P. girvanensis*, with fewer axial rings. It bears some resemblance to the specimen of *Paracybeloides* figured by Whittington & Williams (1955, pl. 40, fig. 110 only) as *Atractopyge* sp. ind., from the Derfel Limestone of early Caradoc age.

HORIZON AND LOCALITY. Lower Melmerby Beds, Lower Longvillian Substage, Alston Road, locality J (see Text-fig. 5).

Family DALMANITIDAE Reed, 1905

Subfamily DALMANITINAE Reed, 1905

Genus ***DALMANITINA*** Reed, 1905

TYPE SPECIES. *Dalmania socialis* Barrande, 1852 by original designation of Reed (1905*a* : 224).

Dalmanitina mucronata (Brongniart) ***matutina*** subsp. nov.

(Pl. 12, figs. 1, 5, 6, 9, 12)

1959*a*. *Dalmanitina* sp. nov., Dean, pp. 204, 208.

DIAGNOSIS. Subspecies of *Dalmanitina mucronata* (Brongniart), characterized by smaller fixigenal spines ; palpebral lobes developed from opposite mid-points of first glabellar lobes to corresponding position opposite third glabellar lobes ;

pygidium, excluding terminal spine, broader than long, with eight axial rings and seven pleurae.

DESCRIPTION. *Dalmanitina mucronata* (Brongniart) has been figured and described in detail by Temple (1952). The cephalon of the new subspecies resembles that of *D. mucronata* in all save two respects. The more important of these is the length of the palpebral lobes which, in *D. mucronata matutina*, extend from just outside the axial furrows, slightly in front of the mid-points of the first glabellar lobes, backwards and slightly outwards until almost opposite the mid-points of the third glabellar lobes. In *D. mucronata* itself the palpebral lobes extend backwards from the first glabellar furrows until level with, or slightly behind, the second glabellar furrows. Only one specimen of the new subspecies has been found with part of the fixigenal spine preserved, but the latter appears to be smaller than that of *D. mucronata*.

The hypostoma and thorax are not known.

The pygidium is subparabolic in outline, broader than long. The most complete specimen, excluding the articulating half-ring and terminal spine, is 18 mm. broad and about 11 mm. (estimated) long. The axis occupies just over one-quarter of the frontal breadth, about four-fifths of the median length (excluding terminal spine), and is bounded by straight axial furrows which converge backwards and die out alongside the terminal piece. There are eight axial rings, the first three of equal length (*sag.*), the remainder becoming successively shorter. The articulating furrow and the three succeeding ring furrows are moderately broad (*sag.*) and fairly shallow medially, but become narrow abaxially and deepen to form apodemal pits. The remaining ring furrows are of more uniform depth but become shallower from the fourth furrow onwards, and the seventh and eighth furrows do not quite attain the axial furrows on the internal mould. The terminal piece is subtriangular in plan and passes backwards into a well-developed, post-axial ridge which runs, in turn, into a stout, upturned, terminal spine. The pleural lobes are gently convex dorsally, ending abaxially in smooth margins where there is a narrow doublure of apparently uniform breadth. Each lobe carries seven pleurae, the first three of which are separated by faintly-impressed, interpleural furrows and ornamented by deep, pleural furrows which curve gently and abaxially backwards. The remaining pleural and interpleural furrows are of about equal depth but become slightly less impressed towards the tip of the pygidium. On the internal mould all these furrows end abruptly at the proximal margin of the doublure, but on the external mould they may be traced, in a much attenuated condition, to the lateral margin, coincident with a poorly-defined border. The test of the entire pygidium, including the terminal spine, is smooth.

Apart from having a smaller number of axial rings than the pygidium of *D. mucronata*, eight as compared with eleven, that of the new subspecies differs also in being relatively broader, almost semicircular in outline, with fewer pleurae, seven compared with eight or nine, whilst the terminal spine is stouter and perhaps longer.

HORIZON AND LOCALITIES. Most of the type-specimens are from Dufton Shales near the top of the Pusgillian Stage in Swindale Beck, locality B. 25. One of the paratypes, however, is from Pus Gill, locality A. 7, where the horizon is low in the

Pusgillian, not far above its presumed junction with the underlying Onnian Stage. Another specimen has been collected by Mr. M. Mitchell from Pusgillian strata in the section at Hurning Lane, 700 yards north-east of St. Cuthbert's Church, Dufton.

HOLOTYPE. BM. In. 49915 (Pl. 12, fig. 6).

PARATYPES. BM. In. 50112 (Pl. 12, fig. 1) ; In. 50113 (Pl. 12, fig. 5) ; In. 49919 (Pl. 12, fig. 9) ; In. 50114 (Pl. 12, fig. 12).

Subfamily ACASTINAE Delo, 1935

Genus ***KLOUCEKIA*** Delo, 1935

TYPE SPECIES. *Phacops phillipsi* Barrande, 1846 by original designation of Delo (1935 : 408).

Subgenus ***Phacopidina*** Bancroft, 1949

TYPE SPECIES. *Phacopidina harnagensis* by original designation of Bancroft (1949 : 310).

Kloucekia (Phacopidina) apiculata (M'Coy)

(Pl. 12, fig. 11)

1851. *Portlockia ? apiculata* M'Coy *in* Sedgwick & M'Coy, p. 162.
1910. *Phacops apiculatus* Salter : Reed, p. 211.
1961*a*. *Kloucekia* (*Phacopidina*) *apiculata* (M'Coy) Dean, p. 324, pl. 2, figs. 6–9, 12. Includes full synonymy of the species.

Several specimens of this characteristic middle Caradoc trilobite have been found in the vicinity of the Alston Road, north-east of Melmerby. The remains are usually fragmentary but may sometimes include articulated thoracic segments. The material agrees closely with the descriptions given by Harper (1947 : 169) and later by Dean (1961*a* : 324), but the individuals, which occur in ashy mudstones, are somewhat smaller than typical North Welsh specimens and significantly smaller than those from south Shropshire, perhaps the result of a less favourable environment.

HORIZONS AND LOCALITIES. *Kloucekia apiculata* has been collected from the Lower Melmerby Beds, Lower Longvillian Substage, of the Alston Road outcrop (see Text-fig. 5) at localities B, C, E, F, G and J, and from the Upper Melmerby Beds, Upper Longvillian Substage, of the same section at locality H. The species has been found nowhere else in the Cross Fell Inlier.

Genus ***DUFTONIA*** Dean, 1959

TYPE SPECIES. *Duftonia lacunosa* by original designation of Dean (1959 : 143).

Duftonia lacunosa Dean

(Pl. 12, fig. 3)

1948. *Pterygometopus* sp., Bancroft *in* Lamont, p. 468.
1959. *Duftonia lacunosa* Dean, p. 144, pl. 19, figs. 1–3, 5, 6, 8.
1959*a*. *Duftonia lacunosa* Dean : Dean, pp. 203, 204, 208.

The species has already been described in detail. All the type-specimens are from the uppermost part of the Dufton Shales, Pusgillian Stage, at Swindale Beck, locality B. 25, but other specimens have been found, though less commonly, at locality B. 24 ; in Pus Gill, locality A. 22 ; and at Hurning Lane, north of Dufton. At both the latter localities the horizon is apparently somewhat lower in the Pusgillian than are the rocks of the type-locality.

HOLOTYPE. BM. In. 49824 (Pl. 12, fig. 3).

PARATYPES. BM. In. 49821 ; In. 49826 ; In. 49830 ; In. 49920.

Family PTERYGOMETOPIDAE Reed, 1905

Subfamily PTERYGOMETOPINAE Reed, 1905

Genus ***CALYPTAULAX*** Cooper, 1930

TYPE SPECIES. *Calyptaulax glabella* by original designation of Cooper (1930 : 387).

Calyptaulax planiformis sp. nov.

(Pl. 13, figs. 1–5)

1891. *Phacops brongniarti* Portlock, Nicholson & Marr, p. 505.
?1945. *Calyptaulax* sp., Størmer, p. 418, pl. 4, fig. 10.
1959*a*. *Calyptaulax* aff. *norvegicus* Størmer : Dean, pp. 204, 208.

DIAGNOSIS. Glabella slightly longer than broad, pentagonal in outline, bluntly pointed frontally attaining maximum breadth across frontal globe. Three pairs of glabellar lobes ; first and second pairs conjunct laterally, third lobes small, almost separated from remainder of glabella. Eyes long, crescentic in plan, extending from opposite first glabellar lobes almost to pleuroccipital furrow. Pygidium subtriangular in plan, broader than long, with large facets, and terminates in blunt point. Tapering axis with seven to ten axial rings ; pleural lobes with six pleural furrows.

DESCRIPTION. Entire cephalon unknown. The glabella is only slightly convex, even in uncrushed specimens, pentagonal in outline, broadly pointed frontally, the length, excluding occipital ring, being slightly greater than the maximum breadth. The frontal lobe is alate, extending laterally as far as the anterior ends of the first glabellar lobes ; there it meets the axial furrows, which diverge forwards at about 30 degrees. The first glabellar furrows are only moderately deep, slightly sigmoidal, and widely divergent anteriorly ; the first glabellar lobes are long and trapezoidal in outline. The second glabellar furrows are shallow, curved, convex forwards, and directed slightly backwards, not reaching the axial furrows, so that the distal ends of the first glabellar lobes are continuous with the smaller, backwardly-directed, second glabellar lobes. The third glabellar furrows are deep, with apodemes, diverge backwards and almost isolate the third glabellar lobes which are thus present only as semi-detached tubercles at the distal ends of the basal glabellar segment. The occipital ring is long (*sag.*), especially medially, moderately broad, and convex forwards with occipital lobes developed abaxially ; it is separated from the glabella by the occipital furrow which is shallow medially but deepens laterally, where it is indented by the third glabellar lobes. The fixigenae are broad and level with long, crescentic, palpebral lobes which are separated from the cheeks by conspicuous palpebral furrows extending from the front of the first glabellar lobes to the pleuroccipital furrow. The pleuroccipital segment is preserved in only one specimen (Pl. 13, fig. 2); the pleuroccipital furrow becomes shallower laterally, not reaching the lateral margin, and the genal angle is rounded. The anterior branches of the facial suture follow the outline of the glabella and no preglabellar furrow is developed, whilst the posterior branches curve gently forwards from behind the palpebral lobes before curving backwards to meet the lateral margins.

The hypostoma and thorax are unknown.

The pygidium is roughly triangular in outline, the length approximately two-thirds the breadth, with gently convex lateral margins which taper posteriorly to a blunt, slightly upturned point. The axis tapers backwards fairly sharply and carries seven to ten axial rings which diminish posteriorly in size and in degree of definition. Beyond the tip of the axis there is a low, postaxial ridge. The pleural lobes are only moderately convex and carry six pleural furrows which decrease in depth from first to sixth, extend just over half-way from the axial furrows to the lateral margin, and become progressively less divergent backwards. The first pleural furrows are truncated distally by a pair of large facets. The first rib furrows are deep, extending rather more than half the breadth of the pleural lobes to cut the lateral margins, and are directed sharply backwards laterally. Subsequent rib furrows are only faintly impressed, though about three can usually be traced at the margin.

HORIZONS AND LOCALITIES. In the Cross Fell Inlier *Calyptaulax planiformis* appears in small numbers in the *Onnia gracilis* Zone of the Onnian Stage, has not yet been found in the *Onnia superba* Zone, probably as the result of inadequate exposures, and becomes more common in the Pusgillian. Most of the type specimens are from the Pusgillian at Swindale Beck, locality B 25, but one paratype is from the *Onnia gracilis* Zone at Pus Gill, locality A. 12. Another locality where the species is known to occur is Pus Gill, locality A. 6, also in the Pusgillian Stage.

HOLOTYPE. BM. In. 50138 (Pl. 13, fig. 4).

PARATYPES. BM. In. 49903 (Pl. 13, fig. 3); In. 49907 (Pl. 13, fig. 5); In. 49908 (Pl. 13, fig. 2); In. 49965 (Pl. 13, fig. 1).

DISCUSSION. *Calyptaulax planiformis* is clearly related to the approximately contemporaneous *C. norvegicus* Størmer (1945 : 417, pl. 4, figs. 2, 3), a species which may possibly be synonymous with *Calyptaulax* [*Homalops*] *altumi* (Remelé) figured by Wiman (1908, pl. 8, figs. 7–10) from the Baltic region. *C. planiformis* differs from *C. norvegicus* in the following respects: the glabella is proportionately longer and less rounded frontally; the axis of the pygidium is longer; the rib furrows are definitely, though generally faintly, defined at the pygidial border, contrasting with the smooth border described by Størmer (1945 : 418). In the last feature the Cross Fell species resembles more the pygidium figured by Størmer (1945, pl. 4, fig. 10) as *Calyptaulax* sp.

Although *Calyptaulax* was once thought to be a predominantly North American genus it is now known from several places in northern Europe and Scandinavia.

In addition to the Norwegian and Baltic records mentioned above, Jaanusson (1953 : 102–103) has recorded *Homalops* (= *Calyptaulax*) cf. *altumi* Remelé from the Slandrom Limestone, *Pleurograptus linearis* Zone, of southern Sweden.

Calyptaulax actonensis Dean (1961*a* : 328) from the Actonian and basal Onnian Stages of south Shropshire strongly resembles the new species, particularly in the form of the cranidium, but the pygidium is slightly shorter, has a shorter axis with fewer axial rings, possesses more strongly defined pleural furrows, and terminates in a better-developed, pointed, caudal spine.

Of the other comparable species of the genus, *Calyptaulax compressa* (Cooper, 1930, pl. 5, figs. 7, 8) has a shorter glabella and smaller fixigenae than has *C. planiformis*, and the pygidium of *C. glabella* (Cooper, 1930, pl. 5, figs. 9–11) is both broader and more pointed posteriorly. *Calyptaulax schucherti* from the Cape Calhoun Formation of northern Greenland (Troedsson, 1929, pl. 19, figs. 17–20) may be distinguished from the new species by its shorter frontal glabellar lobe, and smaller fixigenae and first glabellar lobes.

Genus ***ESTONIOPS*** Männil, 1957

Estoniops comprises phacopid trilobites generally resembling *Pterygometopus* (*s.s.*) but differing essentially from that genus in their lack of a preglabellar furrow. The frontal lobe of the glabella is large and broad, and the first glabellar lobes are relatively large, but the second and third glabellar lobes are much reduced in size. The genal angles are rounded. The surface of the glabella is covered with coarse tubercles, but that of the cheeks is pitted. The pygidium is generally similar to that of *Pterygometopus*, the tip being bluntly rounded, and has a smooth border.

Estoniops has been found in Britain only in the Upper Longvillian Substage of the Anglo-Welsh area but the genus is widely distributed geographically and is known from Scandinavia and the Baltic region. These extra-British occurrences appear to be roughly contemporaneous with, or somewhat earlier than, the Anglo-Welsh material.

TYPE SPECIES. *Acaste exilis* Eichwald, 1857 by original designation of Männil (1957 : 386).

Estoniops alifrons (M'Coy)

(Pl. 12, figs. 2, 4, 7, 8, 10, 13, 14)

1851. *Phacops* (*Phacops*) *alifrons* M'Coy *in* Sedgwick & M'Coy, p. 159, pl. 1G, figs. 12–14.
1852. *Phacops* (*Phacops*) *alifrons* M'Coy : Salter, p. *ii*.
1853. *Phacops jukesi* Salter, p. 11.
1864. *Phacops* (*Acaste*) *alifrons* M'Coy : Salter, p. 33, pl. 1, figs. 31–34.
1864. *Phacops* (*Chasmops* ?) *jukesii* Salter : Salter, p. 36, pl. 1, figs. 29, 30.
1873. *Phacops* (*Acaste*) *alifrons* M'Coy : Salter, p. 52.
1891. *Phacops* (*Acaste*) *alifrons* M'Coy : Woods, p. 149.
1922. *Pterygometopus jukesii* (Salter) Elles, pp. 150, 152, 170.
1923. *Phacops* (*Pterygometopus*) *jukesii* Salter : King, p. 491.
1933. *Pterygometopus jukesi* (Salter) : Bancroft, table 1.
1945. *Phacops* (*Calliops*) *jukesi* Salter : Reed, p. 315.

1959. *Estoniops jukesi* (Salter) Dean, p. 146.
1959*a*. *Estoniops jukesi* (Salter): Dean, pp. 194, 207, 220.
1961*a*. *Estoniops alifrons* (M'Coy) Dean, p. 320.

The species was founded by M'Coy (*in* Sedgwick & M'Coy, 1851 : 159) on three syntypes, now in the Sedgwick Museum. One of these, numbered A. 42694 (Sedgwick & M'Coy, 1851, pl. 1G, fig. 12), is chosen here as lectotype and is refigured (Pl. 12, fig. 4). It comprises a damaged, incomplete cephalon which has undergone slight lateral compression, so that the glabella appears more elongated than is normally the case. The specimen was said to be " from the impure limestone of Capel Garmon " (Denbighshire), a horizon presumed to be of Upper Longvillian age. The remaining syntypes comprise two pygidia, said to be from the " Limestone of Pont y Glyn, Diffwys " (Denbighshire). One of them, Sedg. Mus. A. 42695 (Sedgwick & M'Coy, 1851, pl. 1G, fig. 13), is incomplete and probably slightly crushed, whilst the other, A. 42696 (Sedgwick & M'Coy, 1851, pl. 1G, fig. 14), is a complete pygidium, preserved as an internal mould which is believed to have undergone slight longitudinal compression and is therefore thought to be unsuitable for systematic description owing to the exaggeration of the pleural furrows.

Phacops jukesi Salter (1853 : 11), a species regarded here as a synonym of *Estoniops alifrons*, was established using two syntype cephala from the Bala district. These are in the Geological Survey & Museum where they are numbered 19165 and 19166.

Owing to the poor state of preservation of the type specimens of *Estoniops alifrons* the following description is founded also on supplementary material from both the Bala district, north Wales, and the Cross Fell Inlier.

DESCRIPTION. The cephalon is strongly convex, of semi-elliptical form, broader than long. The glabellar outline is slightly convergent from the posterior border as far as the outer ends of the second glabellar furrows, but then expands rapidly forwards, attaining its maximum breadth a short distance in front of the first glabellar furrows. The glabella is slightly broader than long and there is no preglabellar furrow. The frontal lobe is convex, strongly alate, its projected length in an uncrushed specimen being about two-fifths that of the glabella. The first glabellar furrows are moderately deep, directed backwards slightly and extending adaxially about one-quarter to one-third of the glabellar breadth. The second glabellar furrows are deep, short (*tr.*), directed forwards slightly so that the first glabellar lobes are almost subtriangular in outline. The second glabellar lobes are small, directed backwards, bounded posteriorly by deep third glabellar furrows. The third glabellar lobes are merely the swollen ends of what may be described as a ring-like segment, corresponding in position with the occiput or peduncle of the Trinucleidae and separated by a well-defined occipital furrow from the convex occipital ring, which is slightly wider (*tr.*) than is the glabella across the basal lobes. The axial furrows are narrow and deep, becoming shallower opposite the first glabellar lobes, with hypostomal pits situated opposite the first glabellar furrows. From the posterior margin as far as the second glabellar lobes, the axial furrows converge slightly but then diverge markedly until just beyond the first glabellar furrows, whence they coalesce with the lateral marginal furrows ; the latter run back as far as the distal ends of the pleuroccipital furrow, towards which they become considerably shallower. The eyes are prominent, standing as high as, or slightly higher than, the glabella, and the fixigenae are declined steeply towards the axial furrows. The eye of one of the Cross Fell specimens contains about 165 lenses arranged in twenty-four vertical rows, each row containing from four to eight lenses, but Welsh specimens have not yet been found sufficiently well preserved for detailed comparison. The palpebral lobes are sharply crescentic in form, bounded by deep palpebral furrows. Each palpebral furrow runs from the axial furrow and turns sharply through a right angle opposite the mid-point of the eye before attaining the posterior end of the latter ; from this point a deep furrow runs immediately below the eye, whilst another furrow curves gently forwards and then laterally backwards, becoming almost obsolete before intersecting the lateral marginal furrow. The anterior branches of the facial suture run obliquely forwards from the eyes to cut the axial furrows just in front of the hypostomal pits ; they then turn sharply inwards to converge and meet in front of the glabella. The posterior branches curve forwards gently from behind the eyes and then straighten before cutting the lateral margins ; they are situated in the furrows already described. The librigenae are fused frontally, and a median suture is not developed. The pleuroccipital furrows are deep and transversely straight but die out before reaching the margin. The pleuroccipital segment widens (*exsag.*) noticeably towards the smoothly rounded genal angles. The test of the glabella is covered with coarse tubercles the surface of which, together with the intervening area, is finely granulate. The surface of the cheeks is pitted, but that of the palpebral lobes, occipital ring, pleuroccipital segment and cephalic border is smooth or finely granulate. The cephalic doublure is similarly ornamented but there is no sharp demarcation between this and the tuberculate upper surface of the cephalon at the line of the facial suture.

The hypostoma and thorax are unknown.

No well-preserved topotype pygidium being yet available for examination, the following description is founded on a pygidium, presumed to belong to the species (Pl. 12, figs. 8, 10), which has been found at Swindale Beck in association with a cephalon of *E. alifrons*. The outline is broadly semi-elliptical, the anterior margin slightly convex forwards, and the tip well rounded. The straight-sided, tapering axis, bounded by deep axial furrows, has seven, well-defined axial rings, followed by two further rings which are less distinct medially. The pleural lobes carry six ribs, separated by deep furrows, with a seventh rib less well defined. Interpleural furrows are only faintly impressed and neither they nor the pleural furrows attain the lateral margin, so that a smooth border results.

HORIZON AND LOCALITIES. Although the horizon of M'Coy's syntypes was not specifically stated, the evidence of all other known occurrences of *Estoniops alifrons* in the Anglo-Welsh area suggests that they must have been collected from strata of Upper Longvillian age. Salter's type material of *Phacops jukesi* in the Geological Survey & Museum is labelled merely " Caradoc " of Gelli Grin, Bala, but all the material of the species from that area contained in the Bancroft Collection at the British Museum (Nat. Hist.) is described as having been collected from the Upper Longvillian substage, presumably from what Bancroft (1933, table 1) termed the *Pterygometopus jukesi* Beds. In her paper on the Bala district Elles (1922 : 150, 152, 170) recorded *Pterygometopus jukesi* from the Gelli Grin Calcareous Ash Series at various localities near Bala. The rocks in which *E. alifrons* occurs at Cross Fell belong to the upper half of the Upper Longvillian substage. The species is uncommon there and has, as yet, been found at only two localities, both in Swindale Beck, B. 7 and B. 10.

Phacops (*Pterygometopsis*) [*sic*] cf. *jukesi* has been recorded from the Pen-y-garnedd Limestone of the Berwyn Hills, North Wales (Wedd *et al.*, 1929 : 44), a horizon now known to contain Upper Longvillian fossils (Whittington, 1938 : 436, 451).

LECTOTYPE, here selected. Sedgwick Mus. A. 42694 (Pl. 12, fig. 4).

PARATYPES. Sedgwick Mus. A. 42695 ; A. 42696.

DISCUSSION. In redescribing the holotype of the type species of *Pterygometopus*, *P. sclerops* (Dalman), Whittington (1950 : 548) sought to restrict the genus to that species and *P. trigonocephala* (Schmidt) on account of their having such features as a distinct preglabellar furrow, set back slightly from the facial suture in front of the glabella, and palpebral furrows which continue behind the eye and then, containing the posterior branches of the facial suture, curve towards the marginal furrows. Other forms usually assigned to *Pterygometopus* were said to be distinct because the preglabellar furrow was not impressed, the glabella and preglabellar field being continuous, and the genus *Estoniops* seems to accommodate these phacopids.

Estoniops shares certain characteristics, such as the absence of a preglabellar furrow and the presence of cheeks with a pitted surface, with the genus *Duftonia* (Dean, 1959) but, in addition to other features, the possession of fixigenal spines and a mucronate pygidium assist in separating the latter generically. *Estoniops alifrons* has many features in common with *E. exilis* Eichwald sp. (Schmidt, 1881 : 86, pl. 1, figs. 18–21 ; pl. 12, fig. 13 ; Wigand, 1888 : 43, pl. 6, figs. 5*a*, *b*) from the Kuckers Shale, Stage C2, of Estonia, a horizon probably slightly earlier in age than the Upper Longvillian, but the cephalon of the British form differs in having a more elongate glabella and more divergent axial furrows. A particularly noticeable feature in both species, and in others assigned to *Estoniops*, is the curiously angular form of the palpebral furrow, that of *E. exilis* having been illustrated by Öpik (1937 : 163, fig. 42). *Phacops* (*Pterygometopus*) *panderi* Schmidt (1881 : 84, pl. 1, figs. 15–17 ; pl. 12, figs. 10–12) from Stage C1 of the Baltic region bears some resemblance to *Estoniops* but differs in having tuberculate cheeks, and it is not known whether this feature is of more than specific significance.

Two specimens figured by *Salter* (1864, pl. 1, figs. 33, 34) as *Phacops* (*Acaste*) *alifrons* can probably be assigned to that species. One of them, GSM 19109 (*Salter*, 1864, pl. 1, fig. 35) is an incomplete cephalon labelled, on the tablet, " Tyn-y-cabled, Pennant " ; the other, GSM 19107, is a somewhat distorted pygidium from " Goetre, Meifod ". The latter, from its general similarity to the Swindale Beck pygidium figured here, almost certainly belongs to the same species and is associated with a cephalon, GSM 19108, which definitely belongs to *E. alifrons*. None of the localities above matches those listed by Salter (1864 : 34) for *Phacops alifrons*.

The specimen recorded in the Oswestry Memoir (Wedd *et* al., 1929 : 61) as *Phacops* cf. *alifrons* from the Ashgill Series of the Berwyn Hills is, in fact, a crushed *Paracybeloides* sp. ; it is numbered RE 938–9 in the Geological Survey & Museum.

The trilobite from the Balclatchie Beds of the Girvan district described by Reed (1945 : 314, pl. 1, fig. 6) as *Phacops* (*Calliops*) *jukesi* var. *vicina* appears to be a typical *Calliops* not unlike *C. brongniarti* (Portlock) and cannot be considered closely related to *Estoniops alifrons*.

Subfamily CHASMOPSINAE Pillet, 1953

Genus ***CHASMOPS*** M'Coy, 1849

TYPE SPECIES. *Calymene odini* Eichwald, 1840 by original designation of M'Coy (1849 : 403).

Chasmops cf. ***extensa*** (Boeck)

(Pl. 13, fig. 8)

1959*a*. *Chasmops* cf. *extensa* (Boeck) : Dean, p. 207.

Three fragmentary pygidia belonging to *Chasmops* of the *extensa* species-group have been recovered from Swindale Beck, but only one is sufficiently well preserved for descriptive purposes. The specimen is about 18 mm. long, and the original maximum breadth is estimated to have been about 27 mm. The axis is narrow, with a frontal breadth of about 5 mm., tapers strongly backwards and ends about 3·5 mm. in front of the tip of the pygidium. There is evidence, obscured by crushing, of a postacial ridge. As far as the state of preservation allows, there appear to be fifteen axial rings. Each pleural lobe carries fourteen ribs, the pleural furrows becoming noticeably shallower near the lateral margin. Each rib usually bears a faintly-impressed interpleural furrow and becomes wider (*exsag.*) abaxially. The ribs become smaller towards the tip of the pygidium, at the same time changing their position relative to the axis until the smallest are almost parallel to the sagittal line.

HORIZON AND LOCALITY. Dufton Shales, believed to belong to the middle portion of the Actonian Stage, at Swindale Beck, locality B. 15. The associated fauna includes *Onnicalymene*, *Remopleurides* and *Onniella*.

DISCUSSION. *Chasmops extensa* has been redescribed by Størmer (1940 : 138, pl. 3, figs. 7–11) whose illustrations of the pygidium show that it possesses fifteen axial rings and fourteen pleural ribs, corresponding with the numbers in the specimen now figured. The type pygidium is, however, much more elongate, and narrowly elliptical in outline, but the specimen is uncrushed whereas those from Cross Fell are flattened in a dark-grey shale. In southern Norway *C. extensa* is characteristic of the Upper Chasmops Shale and Limestone, and in south Shropshire members of the same species are most abundant in the Actonian and Marshbrookian Stages, though appearing earlier, in the Upper Longvillian, and ranging upwards into the lowest part of the Onnian (Dean, 1961*a* : 335).

Chasmops aff. ***maxima*** (Schmidt)

(Pl. 13, fig. 6)

1959*a*. *Chasmops* aff. *maxima* (Schmidt) : Dean, p. 208.

The material consists only of one damaged cranidium, estimated length about 15 mm. It is moderately convex, both longitudinally and transversely, and the axial furrows diverge anteriorly at approximately 40 degrees. The frontal lobe is incomplete but its length is about two-thirds of the estimated breadth. The first glabellar furrows are almost straight, diverging forwards at 110 degrees and deepening towards the axial furrows ; the first glabellar lobes are triangular in outline, their convexity conforming with the remainder of the glabella. The second glabellar furrows converge forwards at about 75 degrees and deepen markedly towards the axial furrows ; the second glabellar lobes are present only as small tubercles. The third glabellar furrows occur as notches separating the second glabellar lobes from those of the third pair, which are represented by tubercle-like projections situated just behind the first glabellar lobes and slightly overlapping the occipital furrow. The latter is transversely straight, deepening towards the axial furrows, near which it contains a pair of apodemal pits. Another pair of apodemal pits is situated at the hind margin of the occipital ring, just inwards from the axial furrows and bordering two small, anteriorly-projecting, occipital lobes. The pleuroccipital furrow is moderately deep and the pleuroccipital segment is fairly narrow (*exsag.*), but the two are only partly preserved. Even though incompletely preserved, the one surviving palpebral lobe is prominent, raised above the level of the glabella and carries a shallow, palpebral furrow. In plan the palpebral lobe extends from a point almost opposite the middle of the first glabellar lobe to one opposite the third glabellar lobe. The fixigena declines steeply from the palpebral lobe to the axial furrow.

HORIZON AND LOCALITY. Dufton Shales in, probably, the higher part of the Pusgillian Stage at Pus Gill, locality A. 28.

DISCUSSION. The species has been discussed in detail by Størmer (1945 : 420) who has pointed out that Schmidt (1881 : 112) founded *C. maxima* on specimens from both the Jewe and Kegel Stages and figured a variety of forms under the one name. The specimen from Pus Gill matches best the specimens of *C. maxima* figured by Størmer from the Tretaspis Shales of Hadeland, though a detailed comparison is not possible with the material available.

Chasmops sp.

(Pl. 13, fig. 12)

1959*a*. *Chasmops* sp., Dean, p. 214.

Two specimens of *Chasmops* have been recovered from the Caradoc Series near Melmerby. One, a cranidium BM. In. 54655, is too badly damaged for detailed examination. The other, an almost complete pygidium In. 54656, is slightly distorted, but the length and breadth are estimated to have been respectively 12 mm. and about 16 mm. The axis possesses eleven axial rings extending almost to the terminal piece which, although damaged, appears to be only partly differentiated from the postaxial ridge. The pleural lobes have ten, or perhaps eleven, ribs some of which bear faint traces of interpleural furrows. The ribs are separated from one another by deep pleural furrows which, as far as can be ascertained, extend to the lateral margins of the pygidium.

HORIZON AND LOCALITY. Lower Melmerby Beds, probably representing as an yet undetermined part of the Lower Longvillian Substage, at the Alston Road section near Melmerby, locality J (see Text-fig. 5).

DISCUSSION. The fragmentary evidence available suggests that the species may be new. It is certainly distinct from the so-called longicaudate forms of *Chasmops*, such as *C. extensa* (Boeck), which are so abundant higher in the Caradoc Series of Shropshire and Norway, and its affinities are more likely to lie with the group typified by *Chasmops conicophthalma* (Sars & Boeck), a species redescribed by Størmer (1940 : 137, pl. 3, figs. 1–6) and characteristic of part of the Caradoc Series in Norway prior to the appearance of *C. extensa*.

Family HOMALONOTIDAE Chapman, 1890

Genus ***BRONGNIARTELLA*** Reed, 1918

TYPE SPECIES. *Homalonotus bisulcatus* M'Coy, 1851 by original designation of Reed (1918 : 322).

Brongniartella minor (Salter)

(Pl. 15, fig. 4 ; Pl. 16, fig. 11)

1852. *Homalonotus bisulcatus* var. *β minor* Salter, p. *v*.
1947. *Brongniartella parva* Harper, p. 165, pl. 6, figs. 7, 8.
1961*a*. *Brongniartella minor* (Salter) Dean, p. 351, pl. 54, fig. 6 ; pl. 55, fig. 11.

A few specimens found at one locality in the Inlier agree in all respects with Salter's species, the lectotype of which, a pygidium, was originally described from the Longvillian Stage of the Bala district, North Wales. Although the outer surface of the test, when preserved, is apparently smooth, internal moulds show a conspicuous granulation due to the infilling of small canals within the test. A similar feature is found in *Brongniartella ascripta* (Reed), described elsewhere in this paper.

HORIZON AND LOCALITY. Upper part of the Corona Beds, Lower Longvillian Substage, *Bancroftina typa* Zone, at Pus Gill, locality A. 3 and Harthwaite Sike, E.3.

Brongniartella ascripta (Reed)

(Pl. 15, figs. 1, 2, 5, 8, 11 ; Pl. 16, fig. 14?)

1910. *Homalonotus ascriptus* Reed, p. 216, pl. 17, figs. 4–8.
1918. *Homalonotus ascriptus* Reed : Reed, p. 272.
1959*a*. *Brongniartella ascripta* (Reed) Dean, p. 214.

Reed's description was founded on a single cranidium, which may be taken as the holotype, supplemented by three additional cranidia and a hypostoma, all of which he regarded only as belonging doubtfully to the species. There seems to be little doubt that these specimens belong to *B. ascripta*. The holotype cranidium is somewhat flattened but retains, nevertheless, a longitudinal, median ridge which is particularly well shown on the anterior half of the glabella. In the same specimen crushing has produced what appear to be large, basal glabellar lobes, but all the uncrushed specimens available show no trace of glabellar furrows. Reed described the test of the cranidium as being covered with closely-set " tubercles ", and considered this feature sufficient to distinguish the species from *Brongniartella bisulcata*, but examination of additional material suggests that the so-called tubercles are, in fact, infillings of canals within the original test, the outer surface of which was probably smooth. The straight lateral and frontal margins of the glabella, with the fairly well-defined anterior border and the median carina, suggest that *B. ascripta* may be grouped with forms such as *Brongniartella minor* (Salter) and *B. minor subcarinata* Dean, rather than with *B. bisulcata* and *B. caradociana* (Dean, 1961*a* : 349). The presumed hypostoma of *B. ascripta* is quite distinct from that of *B. bisulcata* (see Dean, 1961*a*, pl. 54, fig. 9), and such a difference may eventually prove to be of subgeneric, or even generic, significance. The thorax is known only from isolated segments which are not distinguishable from those of *B. bisculata*. The presumed type-locality has yielded a few pygidia believed to belong to the species. The largest and most complete of these, BM. In. 52980, is slightly distorted and has a median length of about 17 mm. The pleural lobes are well segmented with seven, and perhaps eight pairs of pleural furrows, the first pair being noticeably deeper than the rest ; the furrows extend to the lateral margin, near which they become shallower and almost obsolete. The axis of this specimen is not sufficiently well preserved for an accurate assessment of the number of axial rings, but another, incomplete pygidium shows that there are at least seven, and probably more.

HORIZON AND LOCALITIES. It is believed that Reed's original material was obtained from locality J near the Alston Road, north-east of Melmerby; the rocks there are thought to belong to the Lower Melmerby Beds, of probable Lower Longvillian age. Elsewhere along the Alston Road fragments of the species have been collected at localities D, E, F and G, from the Lower Melmerby Beds.

In the main portion of the Inlier, specimens tentatively assigned to *B. ascripta* have been found at locality E. 3, Harthwaite Sike, near Dufton (see Text-fig. 4), in the upper part of the Corona Beds, belonging to the *Bancroftina typa* Zone of the Lower Longvillian. A fragmentary cranidium from this locality is figured (Pl. 16, fig. 14), and a large, distorted pygidium, BM. In. 54651, from the same horizon at locality E. 5 shows traces of eleven axial rings.

In their account of the Cross Fell Inlier Nicholson & Marr (1891 : 510) recorded " *Homalonotus rudis* Salter? " from the Corona Beds at Roman Fell, and the specimens were subsequently given the provisional name of *Brongniartella* cf. *rudis* (M'Coy) (Dean, 1959*a* : 209). More recently it has been pointed out that *Homalonotus rudis*, described originally by M'Coy (*in* Sedgwick & M'Coy, 1851 : 168) from North Wales, is not a recognizable species (Dean, 1961*a* : 355). Nicholson & Marr's specimens from Roman Fell, housed in the Sedgwick Museum and numbered A. 32906–12, are figured here for the first time (see Pl. 15, figs. 3, 6, 7, 9, 10). They are too distorted tectonically for certain identification but are undoubtedly generally similar to *B. ascripta*. The pygidia show eleven or twelve axial rings, and one specimen has eight pairs of pleural ribs, though exaggerated by crushing. The best-preserved cranidium has proportions and a glabellar outline like *B. ascripta* but lacks the median carina, though this could well be due to tectonic causes In the absence of more definite specific features, it has been preferred to figure the Roman Fell specimens merely as *Brongniartella* sp. *B. ascripta* has not yet been recorded outside the Cross Fell Inlier.

HOLOTYPE. Sedg. Mus. A. 29632 (Pl. 15, fig. 11).

Brongniartella bisulcata (M'Coy)

(Pl. 16, fig. 8)

1851. *Homalonotus bisulcatus* M'Coy *in* Sedgwick & M'Coy, p. 168, pl. 1G, figs. 26, 27.

1961*a*. *Brongniartella bisulcata* (M'Coy) Dean, p. 346. This reference contains a full synonymy of the species.

Brongniartella bisulcata has been redescribed in detail from the type-area in south Shropshire (Dean, 1961*a*), and the material from the Cross Fell Inlier exhibits no features not already known. The earliest undoubted occurrence is in the upper half of the Upper Longvillian Substage at Swindale Beck, localities B. 5, 8 and 9. Fragmentary evidence suggests that it may also be found at the same horizon at Harthwaite Sike, locality E. 6. As in Shropshire, *B. bisulcata* is fairly common in the Marshbrookian Stage, at which level it is known from both Swindale Beck, localities B. 11, 14 and 16, and Harthwaite Sike, localities E. 7, 9, 10, 11 and 12. In the north of the Inlier, at the Alston Road outcrop, near Melmerby, fragments of *Brongniartella* occur in the lower part of the Upper Longvillian, but have not proved satisfactorily identifiable. They are undoubtedly close to *B. bisulcata* but may yet prove to belong to *B. ascripta*, a species originally described from adjacent and probably earlier strata.

Brongniartella depressa sp. nov.

(Pl. 16, figs. 1, 7, 10, 13)

1959*a*. *Brongniartella* sp. nov., Dean, p. 208.

DIAGNOSIS. *Brongniartella* with glabella of low convexity, poorly defined both laterally and frontally, where outline narrows towards transversely-truncated, frontal, glabellar lobe. Occipital furrow almost absent from external mould. Axial furrows of thorax almost obsolete. Pygidial axis broad, poorly defined; axial rings and pleural ribs scarcely discernible.

DESCRIPTION. The cephalon is known only from a flattened cranidium, the median length of which is slightly less than half the maximum breadth. The glabella is slightly longer than wide, poorly defined laterally by markedly shallow axial furrows which are shallowest and straight frontally, but which then curve outwards and back from about their mid-points to the ends of the occipital ring. The dimensions of the holotype cranidium are as follows: max. length 16 mm., max. breadth 30 mm. (estimated) ; length of glabella 12·5 mm., max. breadth 11 mm., min. breadth 7·5 mm. The convexity of the glabella is remarkably low and the frontal glabellar lobe has a noticeably square appearance, being truncated by a poorly impressed, transversely straight, preglabellar furrow which meets the axial furrows almost at right-angles, the anterolateral angles of the frontal lobe being slightly rounded. The external mould of the holotype shows no trace of glabellar furrows but a presumably immature specimen (Pl. 16, fig. 13) carries three pairs of faintly-marked, almost equispaced, glabellar furrows on the internal mould, whereas the external mould of the same specimen shows no sign of lobation. The anterior border is slightly inclined forwards, transversely straight, uniformly broad (*sag.*), and is not well differentiated from the frontal glabellar lobe. The occipital furrow of the holotype is practically obsolete and the dorsal surface of the glabella is almost continuous with that of the occipital ring ; these two structures are uniformly broad (*tr.*) and the occipital ring is not obliquely truncated distally as, for example, is that of *Brongniartella bisulcata* (M'Coy). The internal mould of an immature cranidium, mentioned earlier, has a transversely straight, moderately-deep, occipital furrow (see Pl. 16, fig. 13) but the external mould of this specimen is almost smooth, comparable with the holotype. On both internal and external mould the pleuroccipital furrow is only moderately impressed, curving gently forwards laterally and delimiting a pleuroccipital segment of almost uniform breadth (*exsag.*). The genal angles are imperfectly known but appear to be rounded. Frontally the fixigenae are narrow, constricting forwards slightly and almost coalescing with the distal ends of the anterior border, from which they are separated by only shallow depressions representing the extension of the preglabellar furrow The posterior portions of the fixigenae are moderately declined, their breadth (*exsag.*) between one-quarter and one-third of the glabellar length. The palpebral lobes are small, short, situated opposite the mid-point of the glabella, and are moderately declined towards the axial furrows. The anterior branches of the facial suture are straight, converging forwards slightly so as to cut the anterior margin just outside the line of the axial furrows. The posterior branches are transversely straight at first but quickly turn backwards strongly to cut the genal angles in a normal gonatoparian position. The eyes, librigenae and hypostoma are not known.

Only one specimen of the thorax attributed to this species is known ; it is incomplete but there are traces of at least ten thoracic segments. The axis is only slightly convex, occupies approximately one-third of the total breadth, and is defined by almost obsolete axial furrows. The pleurae are transversely straight for the most part, but turn down and backwards distally, ending in bluntly-rounded tips. Each pleura carries a large anterolateral facet, delimited by a narrow, raised ridge running from the anterior margin, approximately mid-way between the axial furrow and the fulcrum, towards the posterolateral corner of the tip. Just outside the axial furrow, the frontal margin of each pleura is cut by a slit-like pleural furrow which runs outwards and slightly back so as to intersect the frontal margin mid-way between the fulcrum and the pleural tip.

One, almost complete pygidium ascribed to *B. depressa* is known, preserved as an external mould (Pl. 16, fig. 10). It is of depressed form, and broader than long in the ratio 4 : 3 as far as measurements are possible. The frontal margin is moderately convex forwards and the posterior margin is broadly subparabolic in plan, with a rounded tip. The axis is broad, more than one-third the frontal breadth, defined laterally by faint axial furrows which are moderately convergent posteriorly. There are six or seven, almost indistinguishable, axial rings, followed by a short terminal piece which tends to merge into the posterior border, and there is no postaxial ridge. The pleural lobes are almost smooth, showing only traces of five pairs of pleural furrows, of which the first pair is the most clearly defined.

Internal moulds show a fine granulation probably resulting from the infilling of small canals within the test, but the exterior of the exoskeleton, though apparently smooth, proves, on magnification, to be markedly and finely punctate, the punctation extending even across the various furrows impressed on the dorsal surface.

HORIZON AND LOCALITY. A thin band of fossiliferous, weathered, impure limestone in the higher beds of the Dufton Shales, Pusgillian Stage, at Swindale Beck, locality B. 25.

HOLOTYPE. BM. In. 49882 (Pl. 16, fig. 1).

PARATYPES. BM. In. 49881 (Pl. 16, fig. 7) ; In. 49884 (Pl. 16, fig. 10) ; In. 49885 (Pl. 16, fig. 13).

DISCUSSION. The flattened form and lack of well-defined furrows on the external surface of the test readily distinguish *Brongniartella depressa* from any known species of the genus. Stratigraphically earlier species such as *B. ascripta* and *B. minor subcarinata* frequently exhibit a median carination of the glabella, the latter, together with the thoracic and pygidial axes, being well differentiated by axial furrows, whilst the pleural lobes of the pygidium are better segmented than is the case for *B. depressa*. The glabella of *B. bisulcata* undergoes a marked constriction at about its mid-point, and the anterolateral portions of the frontal glabellar lobe are less angular than those of *B. depressa*. The glabella of *Brongniartella platynota* (Dalman, 1828 : 135 ; Kielan, 1959 : 116, pl. 19, figs. 1–3), like that of the Pusgillian form, shows glabellar furrows only on the internal mould, and the occipital furrow is shallow externally, but the Swedish species has larger fixigenae, a better differentiated glabella which is markedly constricted frontally, and both the ring and pleural furrows of the pygidium are more strongly developed.

Brongniartella aff. ***platynota*** (Dalman)

(Pl. 16, fig. 5)

A single pygidium apparently distinct from coexisting forms in the Pusgillian Stage has been collected from the Dufton Shales in Swindale Beck, locality B 30. It is incomplete, preserved as an internal mould, and possesses at least seven axial rings and five pairs of pleural furrows. The axis is well defined by straight, moderately-deep, axial furrows which are convergent posteriorly, and the pleural lobes are moderately declined laterally. The anterior margin is convex forwards and the pleural ribs are directed backwards, but these features have almost certainly been exaggerated by crushing. Comparison with described species of *Brongniartella* is difficult, but the appearance is generally reminiscent of *B. platynota* (Dalman, 1828 : 135), a form originally described from the Ashgill Series of Sweden and since redescribed by Kielan (195 : 116, pl. 19, figs. 1–3). Each pygidium has a strongly convergent axis and well-defined pleural furrows, and as far as can be judged the number of axial rings and pleural ribs is generally similar.

Family CALYMENIDAE Burmeister, 1843

The first serious attempt to subdivide the trilobites composing this family was made by Shirley who, in 1936, erected several new species and genera, and reviewed previous work on the group. Shirley's genera were later regarded by Richter (1937) as subgenera of *Calymene*, but most are now accepted as being of generic rank. The genus most abundantly represented in the Caradoc Series of the Anglo-Welsh area is that usually referred to as *Flexicalymene* Shirley, 1936, but recently Fisher (1957 : 13) has stated that *Orimops* Rafinesque, 1832, has precedence over the former, and it is necessary to investigate this claim further.

Several North American trilobite species were introduced by Green (1832) who, although he did not figure them, nevertheless gave valid diagnoses and provided sets of plaster casts of his original specimens. Among them was *Calymene callicephala* (Green, 1832 : 31), said to be from Hampshire, Virginia, a species which Rafinesque (1832 : 72), later in the same year, considered to be sufficiently distinct as to warrant the formation of a new subgenus of *Calymene* which he named *Orimops*, though he misspelt the specific name as *calicephala*. Many of Green's species are readily recognizable from their plaster casts, but that of *Calymene callicephala* is not one of the best, and the species is obviously in need of redescription. Consequently *Orimops* must be regarded as a *nomen dubium*, and may eventually prove to be best rejected. Nevertheless, the cast of *C. callicephala* shows enough of the structure of the cephalon to suggest that the species is similar in many respects to the well-known Cincinnatian trilobite *Calymene meeki* (Foerste, 1910 : 84, pl. 3, fig. 18; 1919, pl. 18, fig. 3), a form usually put in *Flexicalymene*, and in his original description of *C. callicephala* Green (1832 : 31) stated that his species occurred near Cincinnati, Ohio, though not at Trenton Falls. Both species are characterized by a markedly triangular glabellar outline, the sides of which are strongly convergent frontally to a narrow, frontal, glabellar lobe, and by the forward position of the eyes which, as in *Platycalymene*, are sited opposite the first pair of glabellar lobes. These two species, together with a closely similar form in the Ashgill Series of Scotland (Shirley, 1936, pl. 29, fig. 8), are regarded here as forming a compact group, both geographically and stratigraphically distinct. The name *Orimops*, if it is to be employed at all, is best used for these species, though the erection of a new name may prove necessary.

The genus *Flexicalymene* was founded by Shirley (1936 : 395) on the well-known south Shropshire trilobite *Calymene caractaci* Salter, 1865, one of several species in which the eyes are situated opposite the second glabellar lobes. Fisher's (1957, pl. 33, fig. 12) use of *Orimops* to include the Trenton trilobite *Calymene senaria* Conrad, 1841, even if the genus were not under suspicion, can hardly be justified and this species is regarded here as belonging to *Flexicalymene* (*s.s.*).

Shirley (1936 : 390–392) regarded the position of the eyes as being constant in most calymenids, and he supposed *Flexicalymene onniensis*, with the eyes situated far back, opposite the third glabellar furrows, to be exceptional. During the present work it has been noted that *F. onniensis* is only one of a number of widely distributed species, again falling within fairly well-defined geographical and stratigraphical limits, in which the eyes are similarly placed, and it is proposed now to separate these as a new genus to which the name *Onnicalymene* is given, with type species *Flexicalymene onniensis* Shirley.

Reacalymene was separated by Shirley (1936 : 395) as a distinct genus and a similar course has been followed by Whittard (1960 : 152, 158). In practice, however, whilst the ridging of the preglabellar field which Shirley claimed as a diagnostic feature is generally obvious, though never strongly developed, on the external mould, when only an internal mould is available all trace of the ridge frequently disappears and it is then impossible to distinguish the specimen from a typical *Flexicalymene*. For this reason it is thought better to follow the course adopted by Whittington (*in* Moore, 1959 : O.452) in regarding *Reacalymene* as being of subgeneric status within the genus *Flexicalymene*. As far as is now known, *Reacalymene* has a relatively restricted vertical range in the Anglo-Welsh area, perhaps through only the lower part of the Caradoc Series. Shirley (1936 : 390) postulated that the first stages in the thickening of the anterior border of the Calymenidae was to be found in *Reacalymene pusulosa* Shirley, from the early Caradoc strata of south Shropshire. This now appears to be an oversimplified view as *Gravicalymene*, with a much more thickened border, is known from the lowest Harnagian Stage, where it is represented by *G. praecox* (Bancroft), and may have existed even earlier.

The position of the calymenids normally placed in *Flexicalymene* may be summarized as follows :

Flexicalymene Shirley, 1936

DIAGNOSIS. Glabellar outline generally subparabolic, rounded frontally. Anterior border moderately long, smooth, usually steeply inclined forwards. Palpebral lobes situated opposite, or almost so, second glabellar lobes. Thorax with thirteen segments (but see later).

DISTRIBUTION. Llandeilo Series to Caradoc Series, probably to highest Marshbrookian Stage. Widely distributed geographically, occurring in England, Wales, Scotland, Ireland, Bohemia and eastern North America.

TYPICAL SPECIES. *F. acantha* (Bancroft), *F. brevicapitata* (Porlock), *F. cambrensis* (Salter), *F. caractaci* (Salter), *F. declinata* (Barrande), *F. forcipata* (M'Coy), *F. planimarginata* (Reed), *F. senaria* (Conrad), *F. shirleyi* Tripp.

Onnicalymene gen. nov.

DIAGNOSIS. Generally similar to *Flexicalymene*, but distinguished by anterior border, which is short and steeply inclined forwards, and by position of palpebral lobes, opposite third glabellar furrows and frontal portion of third glabellar lobes. Thorax with thirteen segments.

DISTRIBUTION. First encountered in the Actonian Stage of the Caradoc Series in the Anglo-Welsh area, *Onnicalymene* ranges upwards at least into the Pusgillian Stage. Its range in Ashgill strata is not known. Found in England, Wales, Sweden and southern Norway.

TYPICAL SPECIES. *O. jemtlandica* (Thorslund), *O. laticeps* (Bancroft), *O. onniensis* (Shirley), *O. salteri* (Bancroft).

Flexicalymene (Reacalymene) Shirley, 1936

DIAGNOSIS. Generally similar to *Flexicalymene* (*s.s.*) but anterior border bears low, transverse ridge, visible at least on external mould, and glabella is proportionately broader across third glabellar lobes, with sides more convergent forwards, producing triangular outline.

DISTRIBUTION Only confirmed from lower part of Caradoc Series in Welsh Borders, but possibly also in Llandeilo Series.

TYPICAL SPECIES. *F.* (*R.*) *limba* (Shirley), *F.* (*R.*) *pusulosa* (Shirley).

British Species of Doubtful Systematic Position

Calymene quadrata (King, 1923 : 504, pl. 26, figs. 1, 2), from the Ashgill Series, is generally referred to *Flexicalymene* but differs considerably from that genus in its glabellar outline, and is unique in having only twelve thoracic segments. Its position and affinities are therefore regarded as being doubtful.

Calymene (*Diacalymene*) *bigener* (Reed, 1935 : 47, pl. 1, fig. 3), from the Ashgill Series of Girvan, has been placed tentatively in *Reacalymene* by Shirley (1936 : 418), but such a position is doubtful and the species needs to be redescribed.

Calymene (*Ptychometopus*) *grayae* (Reed, 1935 : 45, pl. 1, figs. 13, 19?), from the Craighead Limestone, cannot be considered a recognizable species.

Calymene (*Colpocoryphe*?) *aldonensis* (Reed, 1935 : 48, pl. 1, figs. 14, 15), from the *Didymograptus superstes* Shales (= *Nemagraptus gracilis* Zone) of the Girvan district, has been placed in *Flexicalymene* by Shirley (1936 : 418), but the position of the eyes is reminiscent of that in *Onnicalymene*, whilst the glabellar outline is unlike that of any other described species of *Flexicalymene*.

Diacalymene and ***Gravicalymene***

The typically Upper Ordovician or Silurian genus *Diacalymene* Kegel, 1927 has been reported from the Caradoc Series of south Shropshire, supposedly being represented by *D. praecox* Bancroft, 1949, but the species in question is considered here to be better placed in *Gravicalymene* Shirley, 1936. The two genera bear a considerable resemblance to one another in glabellar outline and it is sometimes difficult to differentiate between the respective anterior borders, which were described by Shirley (1936 : 395) as being " roll-like " in *Gravicalymene* and " ridged " in *Diacalymene*. The writer's observations suggest that whereas the type species of *Diacalymene*, *D. diademata* (Barrande), from the Silurian of Bohemia, possesses a distinctive, ridged, steeply-inclined anterior border, those Ordovician species customarily assigned to the genus have an anterior border which is not markedly different from that of *Gravicalymene*, a genus which did not undergo much modification even as late as the Devonian. A more important criterion for separating the two genera is the presence or absence of what Shirley called " papillate second glabellar lobes ", accompanied by " buttresses " on the fixigenae opposite the same lobes. Stumm & Kaufmann (1958 : 949) have drawn attention to the unsuitability of this terminology, and it is suggested that one might more appropriately speak of " conjugate second glabellar lobes and genal buttresses " in *Diacalymene*. Hupé (1955 : 245) has attempted to place *Diacalymene* and *Gravicalymene* in separate subfamilies, respectively Calymeninae and Colpocoryphinae, on the basis of their having unconstricted or constricted axial furrows, but such a course seems obviously unworkable. *Diacalymene diademata* differs in some respects from the described Ordovician species of the genus, the latter in turn resembling *Gravicalymene* in glabellar outline. It seems likely that the two genera are closely related, and may have diverged from a common ancestral group earlier in the Ordovician, but more evidence is needed. As restricted in this paper, *Diacalymene* makes its appearance in the Anglo-Welsh area in the Pusgillian Stage of the Cross Fell Inlier, being unknown in Shropshire ; it becomes more abundant in the succeeding Ashgill Series and continues into the lower Silurian. *Gravicalymene*, though ranging as high as the Devonian, is an earlier genus, known with certainty from the Harnagian Stage of the type Caradoc succession but possibly originating still earlier. In Caradoc strata both genera are subordinate in numbers to the widespread *Flexicalymene* and *Onnicalymene*.

Genus ***FLEXICALYMENE*** Shirley, 1936

TYPE SPECIES. *Calymene Blumenbachii* var. *Caractaci* Salter, 1865 by original designation of Shirley (1936 : 395).

Flexicalymene cf. ***caractaci*** (Salter)

(Pl. 13, fig. 10)

1959*a*. *Flexicalymene* cf. *caractaci* (Salter) : Dean, p. 214.

Calymenid remains have been found at several points in the vicinity of the Alston Road near Melmerby, and some of the better preserved are generally comparable with Salter's species. The type-material of *F. caractaci* came from the Upper Cheney Longville Flags, Marshbrookian Stage, of south Shropshire and has been redescribed by Shirley (1931 : 25). In the Cross Fell Inlier only occasional fragments of calymenid trilobites have been collected from the Marshbrookian Stage, and none has proved identifiable. The strata at Melmerby are probably both Lower and Upper Longvillian in age, and the relevant localities there comprise C to J inclusive, and possibly also locality A (see Text-fig. 5). The lectotype of *Flexicalymene planimarginata* (Reed), redescribed by Shirley (1931 : 22) and Harper (1947 : 167), originated from the Lower Longvillian of North Wales. The species has not yet been reported from the Cross Fell Inlier at this horizon, though

Whittard (1960 : 158) has recorded it earlier, from the Soudleyan Stage of the Shelve Inlier.

Genus *ONNICALYMENE* nov.

TYPE SPECIES. *Flexicalymene onniensis* Shirley, 1936. For diagnosis of genus see p. 112.

Onnicalymene onniensis (Shirley)

(Pl. 13, fig. 7 ; Pl. 14, figs. 1, 2, 7, 10)

1936. *Flexicalymene onniensis* Shirley, p. 405, pl. 29, figs. 5–7.
1949. *Flexicalymene onniensis* Shirley : Bancroft, p. 308, pl. 11, figs. 36, 37.
1958. *Flexicalymene onniensis* Shirley : Dean, p. 224.
1959*a*. *Flexicalymene onniensis* Shirley : Dean, pp. 200, 207.
1959*a*. *Flexicalymene* aff. *onniensis* Shirley : Dean, pp. 202, 208.

This well-known Shropshire species occurs in abundance in the Dufton Shales of the Knock-Dufton district of the Cross Fell Inlier. The earliest specimens are from the *Onnia gracilis* Zone at Pus Gill, localities A. 8, 9, 11, 12, 14 and 15, and the species has been found less commonly in the *Onnia superba* Zone, also at Pus Gill, locality A. 5. Specimens are relatively abundant in rocks of the Pusgillian Stage, and do not appear to be restricted to any particular part of the stage. Localities are numerous and include : Pus Gill, localities A. 1, 6, 18, 21, 24, 25–30 ; Swindale Beck, localities B. 22, 24–26, 28, 33, 34 ; Dufton Town Sike, localities C. 2–4 ; and Hurning Lane. Judging from the matrix of the Pus Gill specimen figured by Shirley (1936, pl. 29, fig. 7) it probably originated from the Pusgillian Stage.

Onnicalymene laticeps (Bancroft)

(Pl. 14, figs. 5, 6)

1949. *Flexicalymene laticeps* Bancroft, p. 307, pl. 11, figs. 33, 33*a*.
1959*a*. *Flexicalymene* cf. *laticeps* Bancroft : Dean, pp. 199, 207.

Fragments referable to this characteristic south Shropshire form have been recovered from locality B. 15 in the bed of Swindale Beck, near the eastern bank, and the best preserved, a cephalon with three attached thoracic segments, is figured here. In Shropshire *O. laticeps* has been found only in the Actonian Stage, particularly the middle third, and the associated fauna at Swindale Beck, comprising *Chasmops* cf. *extensa* (Boeck), *Remopleurides* sp. (see p. 127), *Chonetoidea*, *Onniella* and *Sowerbyella*, suggests a similar horizon. Like other members of *Onnicalymene*, *O. laticeps* has the palpebral lobes sited well back, opposite the third glabellar furrows, but is easily separated specifically by the short glabella with its well-rounded, parabolic outline. Bancroft's original account of the species did not describe the pygidium. Two pygidia, numbered BM. In. 50259 and In. 50260, have been found in association with the figured cephalon at Swindale Beck, and are of characteristic calymenid form. The axis has five well-defined axial rings, with faint traces of a sixth, followed by a short terminal piece. Each pleural lobe carries five pleural ribs with faintly impressed rib furrows which deepen distally; the ribs are separated from each other by deep pleural furrows running from the axial furrows to the lateral margins.

Genus ***DIACALYMENE*** Kegel, 1927

TYPE SPECIES. *Calymene diademata* Barrande, 1852 by original designation of Kegel (1927 : 617).

Diacalymene cf. ***marginata*** Shirley

(Pl. 13, fig. 13; Pl. 14, fig. 11)

1936. *Diacalymene marginata* Shirley, p. 415, pl. 29, figs. 19, 20.
1959*a*. *Diacalymene* cf. *marginata* Shirley : Dean, pp. 204, 208.

Diacalymene marginata was described from the Drummuck Group, Ashgill Series, of the Girvan district by Shirley, who also recorded the species from the Ashgill of North Wales and the Cautley district of Yorkshire. The specimens from the Cross Fell Inlier are closely similar to the holotype in most respects, though the glabella may be slightly broader frontally and the anterior border situated a little closer to the frontal glabellar lobe. Such differences may well be due to tectonic causes. This form is known from the topmost beds of the Pusgillian Stage at locality B. 25, and perhaps also B. 34, in Swindale Beck. At both places the horizon is not far below the disconformable base of the Swindale Limestone. Elsewhere in the Inlier *D.* cf. *marginata* has been found at locality A. 27 in Pus Gill; the horizon here is also in the Pusgillian Stage, but is probably lower than those at Swindale Beck, though the relationships of the strata are obscured by strike-faulting.

Genus ***GRAVICALYMENE*** Shirley, 1936

TYPE SPECIES. *Gravicalymene convolva* by original designation of Shirley (1936 : 395).

Gravicalymene jugifera sp. nov.

(Pl. 13, figs. 9, 11; Pl. 14, figs. 3, 4, 8, 9)

1959*a*. *Gravicalymene* sp. nov., Dean, pp. 204, 208.

DIAGNOSIS. *Gravicalymene* with well-rounded frontal glabellar lobe, and glabella which is relatively narrow for genus. Anterior border of cephalon flattened dorsally, its posterior margin ridged, separated by deep, broad (*sag.*) furrow from glabella. Pygidium of characteristic calymenid shape with five axial rings and five pleural ribs.

DESCRIPTION. The cranidium is moderately convex, both longitudinally and transversely, and about twice as broad as long. The glabella is a little broader than long, its sides gently convergent forwards for the most part, but the breadth increases noticeably at the line of the basal glabellar lobes. The frontal glabellar lobe is short, its anterior margin well rounded. There are three pairs of lateral glabellar lobes, those of the first pair being small, tubercle-like, bounded frontally by shallow, slit-like, first glabellar furrows and posteriorly by wider (*exsag.*), deeper, second glabellar furrows. The second glabellar lobes are larger than those of the first pair, and subcircular in plan. The third glabellar furrows are deep, at first directed slightly backwards from the axial furrows but then bifurcating markedly, the anterior branch so formed being the shorter, curving adaxially forwards around the second glabellar lobes. The posterior branches are deeper and turn backwards towards, though they do not attain, the occipital furrow. The third, or basal glabellar lobes are subangular in plan with gently convex distal margins, bluntly pointed frontally, and are constricted proximally by the posterior branches of the third glabellar furrows. The axial furrows are deep, gently sigmoidal in plan, and of generally uniform breadth except posteriorly, where they narrow slightly as they flex around the basal glabellar lobes. There are deep hypostomal pits situated midway between the first glabellar furrows and the line of the front of the glabella. There is no true preglabellar field or furrow present, and the portion of the cranidium immediately in front of the glabella is continuous with the anterior border, the whole being flexed upwards through about a right-angle. The structure so formed carries a ridge, moderately defined medially but dying out laterally, which marks the junction of the smooth, broad (*sag.*), deep furrow immediately in front of the glabella, and the granulate, flattened, moderately-inclined top of the anterior border. The occipital ring is transversely convex, broadest (*sag.*) medially, becoming narrower laterally towards a pair of poorly-defined occipital lobes. The occipital furrow is shallow and transversely straight medially, deepening laterally where it curves backwards slightly to encompass the basal glabellar lobes. The pleuroccipital furrow is broad (*exsag.*), of moderate depth, becoming shallower abaxially; the pleuroccipital segment is narrow proximally, broadening towards the rounded genal angles. The anterior parts of the fixigenae are of uniform breadth, converging forwards slightly, parallel to the axial furrows. The eyes are situated opposite the second glabellar furrows and the front half of the second glabellar lobes. The visual surface has not been found preserved, and the palpebral lobes are moderately declined adaxially, with only traces of palpebral furrows. Poorly-developed eye ridges run obliquely forwards from the palpebral lobes, ending at the axial furrows opposite the first glabellar lobes. The librigenae are of characteristic calymenid type, steeply declined laterally. The hypostoma is unknown.

The thorax is represented by only one crushed example in which the number of thoracic segments is not visible. In spite of the poor state of preservation the segments do not appear to differ significantly from those of other calymenids.

In plan the pygidium is broadly kite-shaped, the anterior margin strongly curved forwards and the lateral margins straight, converging backwards to a blunt point. The axis is convex dorsally, defined laterally by deep axial furrows extending almost to the tip. Excluding the articulating half-ring there are four well-developed axial rings, separated by deep, transversely-straight ring furrows, with a fifth less obvious axial ring, followed by a relatively long terminal piece extending almost to the tip of the pygidium, to which it is linked by a suggestion of a low postaxial ridge. The pleural lobes carry four pairs of well-developed pleural ribs which become progressively less divergent backwards, with traces of a fifth pair almost parallel to one another. The ribs of the first pair have interpleural furrows only on the distal half of the dorsal surface, but on the remaining pairs the interpleural furrows extend from just outside the axial furrows to the lateral margins, dividing each rib into two bands, of which the anterior is the narrower (*exsag.*).

Excluding the furrows, which are apparently smooth, the surface of internal moulds is generally finely granulate, representing the infilling of canals within the original test. A little of the test remains on the holotype cranidium, and the inclined, upper surface of the anterior border is finely granulate whilst that of the broad (*sag.*) furrow immediately in front of the glabella is smooth.

Horizon and localities. All the known occurrences of *Gravicalymene jugifera* are in Dufton Shales belonging to the Pusgillian Stage. The holotype is from Swindale Beck, locality B. 28, but the species is known also from Pus Gill, locality A. 24 ; Swindale Beck, localities B. 20, B. 30 and, with some doubt, B. 25 ; Dufton Town Sike, locality C. 6 ; Billy's Beck, locality D. 1 ; and at Hurning Lane, 700 yards north-east of St. Cuthbert's Church, Dufton.

Holotype. BM. In. 50263 (Pl. 14, figs. 3, 4, 8).

Paratypes. BM. In. 50245 (Pl. 13, figs. 9, 11) ; In. 55897.

Discussion. *Gravicalymene jugifera* seems to be closely related to the type-species of the genus, *G. convolva*, which was described from the Ashgill Series of Birdshill Quarry, near Llandilo (Shirley, 1936 : 409, pl. 29, figs. 16–18). The new species may, however, be distinguished by its slightly narrower glabellar outline, smaller basal glabellar lobes, more dorsally flattened anterior border, and by the greater breadth (*sag.*) of the furrow separating the anterior border from the frontal glabellar lobe. Both species have a glabellar outline remarkably close to that found in certain Ordovician species of *Flexicalymene* (*s. l.*) described by Stumm & Kaufmann (1958 : 951, 953, pl. 123, figs. 14, 15 ; pl. 124, figs. 2–16) from Michigan, but are distinguished by the different structure of the anterior border.

Family DIMEROPYGIDAE Hupé, 1953

Genus ***TOERNQUISTIA*** Reed, 1896

Type species. *Cyphaspis* (*Törnquistia*) *nicholsoni* (Reed, 1896 : 433) by monotypy.

Toernquistia aff. ***reedi*** Thorslund

(Pl. 16, figs. 2, 3)

1910. *Törnquistia nicholsoni* (Reed) Reed, p. 211.
1940. *Törnquistia reedi* Thorslund, p. 148, pl. 10, figs. 14–19 ; pl. 11, fig. 15.

Only a small, incomplete cranidium preserved as an internal mould is available. The calculated length is estimated to have been about 2 mm. and the breadth across the palpebral lobes 2·3 mm. The glabella is subparabolic in outline, moderately convex, bounded laterally by deep, narrow, axial furrows which are continuous frontally with the preglabellar furrow. There are no glabellar furrows. The fixigenae are narrow, lower than the glabella and continuous frontally with the preglabellar field. The latter is broad (*exsag.*) distally, but narrows towards the median line where a deep pit is situated in the preglabellar furrow ; from this pit a slot-like depression extends forwards almost half-way across the steeply-declined, preglabellar field. The anterior border is narrow (*exsag.*), almost flat, separated from the preglabellar field by a narrow (*exsag.*), shallow, anterior border furrow. The surviving left palpebral lobe, though incomplete posteriorly, is long and narrow, separated from the fixigena by a broad, shallow, palpebral furrow. In front of the palpebral lobes the anterior branches of the facial suture diverge strongly towards the margin. All the furrows of the cranidium are smooth, but the surface of the anterior border is finely granulate, whilst that of the glabella, palpebral lobes and preglabellar field is covered with small tubercles which increase in size on the distal portions of the fixigenae.

HORIZON AND LOCALITY. Probably that denoted here by the letter J (see Text-fig. 5), east of the Alston Road, north-east of Melmerby. The rocks probably belong to the Lower Melmerby Beds, Lower Longvillian Substage.

DISCUSSION. In emending the Family Dimeropygidae, Whittington & Evitt (1954 : 35) placed therein the genera *Dimeropyge* Öpik, *Dimeropygiella* Ross, *Toernquistia* Reed, *Mesotaphraspis* Whittington & Evitt, and *Chomatopyge* Whittington & Evitt. They noted the species described by Thorslund (1940 : 148) as *Törnquistia reedi*, but considered its generic position to be uncertain owing to its possessing a cephalon recalling that of *Mesotaphraspis* and a pygidium resembling that of *Chomatopyge*. Until more material is available the systematic position of the Alston Road form is debatable. Generically it appears to be closer to *Toernquistia* than to *Mesotaphraspis*, whilst bearing a considerable resemblance to Thorslund's species, though the latter has faint glabellar furrows and a striate anterior border. The type material of *Toernquistia reedi* was obtained from the limestone facies of the Lower Chasmops Limestone, 4bβ, of Jemtland, Sweden, a horizon which may not differ appreciably from that of the Alston Road species.

Toernquistia nicholsoni Reed sp. (1896 : 433, pl. 21, figs. 3, 3*a* ; see also Whittington, 1950 : 561, pl. 75, figs. 8–16), from the Keisley Limestone of Ashill age in the Cross Fell Inlier, differs in having palpebral lobes situated farther forwards, and in being proportionately narrower across the frontal glabellar lobe.

The trilobite originally described by Reed (1904 : 86, pl. 12, figs. 3–7) as *Menocephalus*? (*Törnquistia*) cf. *nicholsoni*, from the Balclatchie Group of Girvan bears a strong resemblance to that from the Alston Road, but differs from the latter in having a more transversely straight, anterior cephalic border, as well as a pair of deep furrows running distally from the mid-points of the axial furrows to just in front of the palpebral lobes. The Balclatchie species was later renamed *Hystricurus translatus* by Reed (1931 : 6), and placed in *Toernquistia* by Whittington (1950 : 563). Hupé (1955 : 143, fig. 124, 6*a*, *b*) has since recorded " *Törnquistia nicholsoni* Reed " from the Llandeilo Series of Scotland, and it must be presumed that his paper refers to *Toernquistia translata*, as no genuine record of *T. nicholsoni* is known from pre-Ashgill strata.

Family ILLAENIDAE Hawle & Corda, 1847

Genus *STENOPAREIA* Holm, 1886

TYPE SPECIES. *Illaenus linnarssoni* Holm, 1882 by original designation of Holm (1886 : 152).

Stenopareia? sp.

(Pl. 16, fig. 12)

1910. *Illaenus Bowmani* [*sic*] Salter (?), Reed, p. 211.

A single pygidium recorded by Reed (1910 : 211) is the only-known representative of the family in the Caradoc Series of the Inlier. The specimen is relatively long, the median length only slightly less than the maximum breadth. *Stenopareia* has been accepted as a distinct genus by Jaanusson (1954 : 570–572), and he has been followed by Whittard (1961*a* : 216, pl. 30, figs, 10–13) who has described a new species, *S. camladica*, from the Lower Soudleyan Stage of west Shropshire. The pygidium of *S. camladica* bears a considerable resemblance to that from the Inlier, but detailed comparison is not possible owing to lack of material.

HORIZON AND LOCALITY. Probably the Lower Melmerby Beds at locality J near the Alston Road (see Text-fig. 5).

Family LICHIDAE Hawle & Corda, 1847

Subfamily HOMOLICHINAE Phleger, 1936

Genus *CONOLICHAS* Dames, 1877

TYPE SPECIES. *Lichas aequiloba* Steinhardt, 1874 by subsequent designation of Vogdes (1890 : 23).

Conolichas melmerbiensis (Reed)

(Pl. 17, figs. 14, 16 ; Pl. 18, figs. 1–4)

1907. *Lichas* (*Homolichas*) *melmerbiensis* Reed, p. 396, pl. 17, figs. 1–7.
1910. *Lichas melmerbiensis* Reed : Reed, p. 211.
1933. *Platylichas melmerbyensis* (Reed) Bancroft, table 2.
1937. *Tetralichas melmerbiensis* (Reed) Phleger, p. 1088.
1939. *Conolichas melmerbiensis* (Reed) Warburg, p. 73.
1946. *Platylichas melmerbiensis* (Reed) : Bancroft *in* Lamont, p. 237.
1948. *Platylichas melmerbiensis* (Reed) : Bancroft *in* Lamont, p. 416.
1958. *Conolichas melmerbiensis* (Reed) : Tripp, p. 576.
1959*a*. *Conolichas melmerbiensis* (Reed) : Dean, pp. 213, 214.

All Reed's type-specimens were described by him merely as having been collected from what he called the Dufton Shales near Melmerby. The manuscript catalogue accompanying the specimens, together with their state of preservation, suggests that the place of origin was locality J, east of the Alston Road, near Melmerby (see Text-fig. 5), and during the present field-work two more specimens of the species have been obtained from this locality. The horizon is in the Longvillian Stage, and the rocks at locality J are believed to belong to the Lower Melmerby Beds, of probable Lower Longvillian age. It was claimed by Bancroft (1933, table 2; *in* Lamont, 1948 : 416) that what he called *Platylichas melmerbiensis* occurred near Melmerby with *Wattsella horderleyensis* Whittington, but the latter, a zonal brachiopod species in the Lower Longvillian of south Shropshire and North Wales, has not yet been confirmed in the Cross Fell Inlier. The type-specimens of *Conolichas melmerbiensis* are unusual in including several whole, or nearly whole, exoskeletons, and it may be that they occurred at only one restricted horizon where conditions were particularly suitable for their preservation.

LECTOTYPE, here selected. Sedg. Mus. A. 29638 (Pl. 18, figs. 3, 4).

PARATYPES. Sedg. Mus. A. 29637 (Pl. 18, fig. 1); A. 29639; A. 29640; A. 29641 (Pl. 17, fig. 16); A. 29642 (Pl. 18, fig. 2); A. 29643 (Pl. 17, fig. 14).

Genus ***PLATYLICHAS*** Gürich, 1901

TYPE SPECIES. *Lichas margaritifer* Nieszkowski, 1857 by original designation of Gürich (1901 : 522).

Platylichas cf. ***laxatus*** (M'Coy)

(Pl. 17, figs. 1, 7)

1959*a*. *Platylichas laxatus* (M'Coy) (s.l.) : Dean, pp. 204, 207, 208.

Lichas laxata was described by M'Coy (1846 : 51, pl. 4, fig. 9) from southern Ireland, and founded by him on an incomplete, compressed cranidium, now in the National Museum of Ireland, from Ballygarvan Bridge, New Ross. The species has since been widely quoted by a number of authors from a variety of horizons within the Caradoc and Ashgill Series, and although it seems likely that more than one species may be present, comparison with other forms will continue to be difficult until a detailed redescription is available on the basis of topotype material. A long description was given by Warburg (1939 : 118) using Scandinavian material of Caradoc and Ashgill age. The cranidia of these specimens appear indistinguishable from each other, and the pygidia exhibit only occasional minor differences which may or may not be of specific significance. The specimens from the Chasmops Limestone of Norway and Sweden cannot reasonably be separated from those now under consideration from the Cross Fell Inlier, particularly when allowance is made for variation within the species.

In the Anglo-Welsh Caradoc Series, *Platylichas* of the *laxatus* type has been found as early as the Derfel Limestone (Whittington & Williams, 1955 : 424, pl. 40, figs. 113–118), whilst the Longvillian strata of North Wales contain remains identical with *Lichas nodulosus* (M'Coy *in* Sedgwick & M'Coy, 1851 : 151, pl. 1F, fig. 16). Tripp (1958 : 579, pl. 85, fig. 5) has refigured the holotype of the latter species and considers it to be synonymous with *Platylichas laxatus*, though pointing out that it may eventually prove to merit subspecific status. The specimen is incomplete but exhibits, nevertheless, a remarkably close resemblance to a pygidium figured here (Pl. 17, fig. 7).

The earliest-known occurrence of *Platylichas* in the Cross Fell Inlier is in the Upper Melmerby Beds of the Alston Road outcrop, locality H (see Text-fig. 5). The sole specimen found (Pl. 17, fig. 2) is a fragmentary pygidium, numbered BM. In. 52595, which belongs unmistakably to the genus but which is insufficient for specific comparison and is accordingly named merely *Platylichas* sp.

The two figured specimens of *Platylichas* cf. *laxatus* (M'Coy) are from the highest beds of the Dufton Shales, Pusgillian Stage at Swindale Beck, locality B. 25. They are numbered BM. In. 50115 (Pl. 17, fig. 1) and In. 50117 (Pl. 17, fig. 7). What is apparently the same form is known earlier, in Dufton Shales of the Onnian Stage, *Onnia gracilis* Zone, at Pus Gill, localities A. 12, 13 and 14.

Family ODONTOPLEURIDAE Burmeister, 1843

Genus *PRIMASPIS* R. & E. Richter, 1917

TYPE SPECIES. *Acidaspis primordialis* Barrande, 1852 by original designation of R. & E. Richter (1917 : 466).

Primaspis semievoluta (Reed)

(Pl. 17, figs, 3, 10, 11, 13, 15)

1910. *Acidaspis semievoluta* Reed, p. 214, pl. 17, figs. 1–3.
1959*a*. *Primaspis semievoluta* (Reed) Dean, p. 214.

All Reed's syntypes are believed to have been obtained from the Lower Melmerby Beds, probably Lower Longvillian Substage, at locality J near the Alston Road (see Text-fig. 5). During the present work one further specimen has been collected from what is believed to be the same geological horizon at locality F beside the Alston Road ; this specimen, a distorted cranidium, is in the British Museum, where it is numbered In. 53000.

Few species of Odontopleuridae are known from the Anglo-Welsh Caradoc Series. *Primaspis harnagensis* (Bancroft, 1949 : 301, pl. 10, figs. 21, 22), from the Harnagian Stage of Shropshire, has a narrower glabellar outline than *P. semievoluta*, and the pygidium has seven pairs of marginal spines, compared with five pairs on the Cross Fell species. One of the paratypes of *P. semievoluta* (see Pl. 17, fig. 10) has a relatively narrow glabella not unlike that of *P. harnagensis*, but this is believed to be the result of tectonic distortion. The lectotype cranidium of *Primaspis semievoluta* bears a noticeable resemblance to that of *Primaspis caractaci* (Salter, 1857 : 211, pl. 6, figs. 15–17), a species found most commonly in the Actonian Stage of south Shropshire. The glabella of the Shropshire form is, however, slightly broader across the basal glabellar lobes, and a little more pointed frontally. The pygidia are more distinct, that of *P. semievoluta* having five pairs of marginal spines, compared with six pairs in *P. caractaci*. In each case the third pair of spines is longer and stouter than the others.

LECTOTYPE, here selected. Sedg. Mus. A. 29951 (Pl. 17, fig. 3).

PARATYPES. Sedg. Mus. A. 29952 (Pl. 17, fig. 10); A. 29953 (Pl. 17, fig. 15); A. 29954 (Pl. 17, fig. 11).

Odontopleurid gen. et sp. ind.

Apart from the occurrence of *Primaspis semievoluta* (Reed) in the Alston Road outcrop, the only other evidence of the family in the Caradoc Series of the Inlier is an unidentifiable fragment from the Dufton Shales, Pusgillian Stage, at Dufton Town Sike, locality C. 6 (see Text-fig. 4), collected by Mr. M. Mitchell. The specimen, BM. In. 51848, is an external mould showing part of the glabella with two pairs of glabellar lobes, the right palpebral lobe, situated opposite the basal glabellar lobe, and a wide (*sag.*) occipital ring carrying a small but well-defined median tubercle. There are traces of three thoracic segments and the surface of the test is ornamented with large closely-set granules. The general aspect is not unlike that of a species of *Primaspis* but the specimen is inadequate for even generic determination.

In describing *Acidaspis magnospina* from the Ashgill Series of the southern Lake District, Stubblefield (1928 : 427) stated that his new species was probably the same as that recorded by Marr (1892 : 108) as " *Acidaspis* n. sp." from the " Sleddale Group of Pusgill and Applethaite ". Earlier, Nicholson & Marr (1891 : 511), in listing the fossils then known from the Dufton Shales, noted " *Acidaspis* n. sp." from " Pusgill " and the specimen is in the Sedgwick Museum, where it is numbered A. 32956. The species is apparently *Acidaspis magnospina* Stubblefield, but the matrix is not that of the Dufton Shales; it resembles instead the lithology of the so-called *Staurocephalus* or Swindale Limestone, a horizon not known from Pus Gill but which crops out at Swindale Beck and Billy's Beck, and the specimen is probably mislabelled.

Family OTARIONIDAE R. & E. Richter, 1926

Genus ***OTARION*** Zenker, 1833

TYPE SPECIES. *Otarion diffractum* Zenker, 1833 by subsequent designation of R. & E. Richter (1926 : 95).

Otarion sp.

(Pl. 17, figs. 4, 12)

? 1891. *Cyphaspis megalops* M'Coy (?) : Nicholson & Marr, p. 509.
1959*a* *Otarion* sp., Dean, p. 214.

Two indifferently-preserved cranidia from the Upper Melmerby Beds, Upper Longvillian Substage, at locality H by the Alston Road, represent the only specimens of the genus known from the Cross Fell Inlier. The more complete example, figured here, bears a general resemblance to the cephalon of *Otarion planifrons* (Eichwald), a Baltic species from the Kuckers Stage which has been refigured by Öpik (1937, pl. 2, figs. 1, 2, text-fig. 2). The proportions of the glabella, and the size and position of the basal glabellar lobes, is similar in both species, but the glabella of *O. planifrons* is the more coarsely tuberculate and possesses a preglabellar field which is slightly longer. *Otarion isoplates* Tripp (1954 : 669, pl. 3, figs. 1–4) has a preglabellar field and anterior border very like those of the Alston Road form but the basal glabellar lobes are slightly larger and project farther abaxially.

Family PROETIDAE Salter, 1864

Subfamily PROETIDELLINAE Hupé, 1953

Kielan (1959 : 69) has declared that the Subfamily Proetidellinae is synonymous with that of the Proetinae, on the grounds that Hupé's subdivision is unsatisfactorily diagnosed, utilizing only the degree of divergence of the anterior branches of the facial suture. The type genera of these two subfamilies differ considerably in several respects, including the presence in *Proetidella* of a definite preglabellar field such as is not seen in *Proetus*. Accordingly the writer prefers to follow Richter & Struve (*in* Moore, 1959 : O.395) in retaining Proetidellinae as a distinct Subfamily.

Genus ***PROETIDELLA*** Bancroft, 1949

TYPE SPECIES. *Proetidella fearnsidesi* by original designation of Bancroft (1949 : 304).

Proetidella? marri sp. nov.

(Pl. 16, figs. 4, 6, 9 ; Pl. 17, figs. 5, 6, 8, 9)

1959*a*. *Proetidella* aff. *fearnsidesi* Bancroft : Dean, p. 206.

DIAGNOSIS. Glabella of approximately equal length and breadth, broadest posteriorly, narrowing frontally to gently rounded frontal lobe. Preglabellar field long, flat ; anterior border brim-like in form, steeply inclined. Palpebral lobes narrow, extending backwards almost to occipital furrow.

DESCRIPTION. The cephalon is known only from discrete cranidia and librigenae. The glabella is roughly as broad as long, gently convex longitudinally and transversely, its line of greatest breadth situated a little way in front of the occipital furrow. The glabellar outline constricts frontally, and glabellar furrows are totally absent. The axial furrows are only moderately deep, converging frontally around the anterolateral angles of the frontal lobe, the anterior margin of which is gently convex, to become continuous with the preglabellar furrow, which is of similar depth. The preglabellar field is flat, fairly long (*sag*), equal to about one-quarter of the length of the glabella, arched forwards gently, and differentiated by only a poorly-defined furrow from the anterior border. The last-named structure forms a conspicuous, raised brim to the front of the cranidium and is generally steeply inclined forwards, though the angle may vary according to the state of preservation. The occipital ring is slightly convex transversely, less so longitudinally, of greatest length (*sag.*) medially but shortening a little laterally where it forms a pair of ill-defined occipital lobes. The hindmost parts of the fixigenae have not been found preserved; frontally they form only a thin, rim-like continuation of the preglabellar field, and medially are not differentiated from the palpebral lobes. The latter are narrow, declined proximally, and extend from opposite the mid-point of the glabella almost to the line of the occipital furrow. The librigenae are known only from dissociated specimens, and the ocular surface of the eye has not been found preserved. Beneath each eye is a poorly-defined eye-platform from which the convex upper surface of the librigena declines steeply to a deep, broad, lateral border furrow; beyond the latter is a well-developed lateral border which passes backwards into a librigenal spine of moderate length. The pleuroccipital furrow is well defined and of moderate depth, intersected by the lateral border furrow without reaching the margin; the pleuroccipital segment becomes broader (*exsag.*) laterally, where it passes without interruption into the librigenal spine. As far as can be judged from both cranidia and librigenae, the posterior branches of the facial suture run laterally back from the posterior end of the eyes to cut the cephalic margin only a short distance outside the axial furrows; the anterior branches converge from the eyes almost to the axial furrows but then curve anterolaterally to cut the anterior border longitudinally in-line with the palpebral lobes

The hypostoma and thorax are not known.

One almost complete pygidium attributed to the species has been collected. The frontal breadth is between two and three times the median length, and the outline is generally semi-elliptical, though the frontal margin is gently curved back laterally. The axis is well defined, the sides converging backwards only gently, and does not quite reach the tip of the pygidium. It is strongly convex transversely and stands well above the pleural lobes, which are only a little declined to the entire lateral margins. It is estimated that there are five axial rings, with a short terminal piece. The most complete specimen has four pairs of pleural furrows, the first pair slightly more impressed than the rest (Pl. 17, fig. 6), and an additional specimen, In. 55880, shows that each of the pleural ribs is divided by a shallow interpleural furrow into two unequal bands, of which the anterior is the narrower (*exsag.*). As far as can be ascertained, both sets of furrows extend to the lateral margin.

The dorsal surface of the glabella, occipital ring and anterior border is covered with thin, slightly-raised, anastomosing ridges arranged in a Bertillon pattern, but the furrows of the cranidium, together with the preglabellar field, are smooth. The librigenae have not been found sufficiently well preserved to ascertain whether they are so ornamented, but the doublure can be seen to be covered with terrace lines subparallel to the lateral margin. The test of the pygidium is not adequately known.

HORIZON AND LOCALITY. Corona Beds belonging to the Lower Longvillian Substage, *Bancroftina typa* Zone, at Harthwaite Sike, locality E. 3, east of Dufton (see Text-fig. 4).

HOLOTYPE. BM. In. 54644 (Pl. 16, fig. 4; Pl. 17, fig. 8).

PARATYPES. BM. In. 54645 (Pl. 17, fig. 5); In. 54646 (Pl. 16, fig. 9); In. 54647 (Pl. 16, fig. 6); In. 54648 (Pl. 17, fig. 9); In. 55880; In. 55881; In. 55882 (Pl. 17, fig. 6).

Discussion. The holotype of *Proetidella fearnsidesi* has recently been refigured in the form of a line drawing by Struve (*in* Moore, 1959 : O. 396, fig. 301, 1) but his illustration is somewhat misleading. The original specimen is preserved as a flattened external mould in shaly mudstone, and the glabella is distorted by crushing. The species is to be redescribed by the writer in a future paper, but in the meantime it may be stated that the presence in Struve's illustration of a bluntly-pointed frontal glabellar lobe, together with a pair of basal glabellar lobes, is the result of crushing. In addition, the pygidium of the holotype has well-defined pleural furrows extending to the lateral margins, as well as traces of interpleural furrows.

In *Proetidella*? *marri* the attributed pygidium is shorter than that of the Shropshire species, with fewer pleural furrows and axial rings, numbering four and five respectively compared with five and seven. The narrowing of the frontal glabellar lobe of the Cross Fell form, together with its more transverse frontal margin, are features not seen in *P. fearnsidesi*. The frontal portion of the cranidium is not easy to compare in the two species owing to differences in the state of preservation, as already stated, but the preglabellar field of *P.*? *marri* is the longer (*sag.*), and its anterior border may be both better differentiated and more steeply inclined.

Of other British Ordovician proetids, "*Proetus*" *girvanensis* (Nicholson & Etheridge, 1878 : 169, pl. 12, figs. 7–10) from the Drummuck Group of Girvan has a shorter (*sag.*) preglabellar field and a larger glabella with three pairs of definite, though poorly-impressed, glabellar furrows. The eyes are also smaller and situated farther forwards. The trilobite described by Reed (1914 : 27, pl. 4, fig. 8) as *Cyphaspis jamesoni* and founded on a single imperfect specimen from the Balclatchie Group, has a cephalic form, including the development of the preglabellar field, not unlike *Proetidella*, but comparison of this species must await its further description.

The genus *Decoroproetus* Přibyl, 1946, with type-species *Proetus decorus* Barrande from the Silurian of Bohemia, was claimed by Přibyl (1953 : 60) as a synonym of *Proetidella*, but is now held to be generically distinct, separable by means of its well-defined basal glabellar lobes, and by the pygidium, the pleural furrows of which are better developed, more numerous, and turn backwards more strongly.

In *Ogmocnemis* from the Ashgill Series of Poland (Kielan, 1959 : 69–71) there are only traces, not always visible, of basal glabellar lobes, the anterior branches of the facial suture are less divergent frontally than in *Proetidella*, and the eyes are somewhat smaller, ending posteriorly a little farther in front of the pleuroccipital furrow. The reasons for separating the two generically may not be well founded, and *Ogmocnemis* may be a subgenus of *Proetidella*, if not actually synonymous with it. Whittard (1961 : 186) has laid stress on the importance of the preglabellar field in proetid classification, and has used Kielan's genus in describing *Ogmocnemis calvus* from the Lower Soudleyan of west Shropshire. It is difficult to distinguish the incomplete type cranidium figured by him from one of *Proetidella fearnsidesi*, and the species may range above the Harnagian Stage. Specimens in the Soudleyan of south Shropshire are almost identical with *O. calvus*, but their apparent differences from *P. fearnsidesi* may be merely the expression of a different lithology and preservation.

Family REMOPLEURIDIDAE Hawle & Corda, 1847

Genus *REMOPLEURIDES* Portlock, 1843

TYPE SPECIES. *Remopleurides colbii* Portlock, 1843 by subsequent designation of Miller (1889 : 565–566).

Trilobite remains broadly referable to this genus have been found at a number of different horizons and localities in the Cross Fell Inlier. In no instance has the hypostoma or pygidium been recovered, and the cranidia are usually damaged or distorted. Consequently it has not proved practical to assign specific names to the specimens or to make a firm comparison with other species, and in the following account they are arranged according to their geological horizons.

Remopleurides sp.

(Pl. 18, fig. 12)

1959*a*. *Remopleurides* sp., Dean, p. 214.

A small damaged cranidium, lacking the anterior glabellar tongue, is the only evidence of the genus in the Lower Melmerby Beds of the Alston Road section, where it was found at locality E. The specimen is too poor for detailed comparison, but the main portion of the glabella is generally similar to that of *Remopleurides biaculeatus*, described by Tripp (1954 : 664, pl. 2, figs. 1–12) from the Craighead Mudstones of the Girvan district.

Remopleurides sp.

(Pl. 18, figs. 6, 10)

1959*a*. *Remopleurides* sp., Dean, p. 214.

A single cranidium has been found in the Upper Melmerby Beds, Upper Longvillian Substage, at locality H by the Alston Road, near Melmerby. It is too badly damaged for comparison with other species, but it is interesting to note that the genus has been recorded by Harper (1956 : 389) from North Wales, in association with an Upper Longvillian fauna. The Alston Road specimen is of relatively large size, the basal breadth of the glabella being approximately 15 mm.

Remopleurides sp.

(Pl. 18, figs. 7, 8)

1959*a*. *Remopleurides* sp., Dean, p. 207.

Two small cranidia have been collected from Dufton Shales believed to belong to the middle portion of the Actonian Stage at locality B. 15 in Swindale Beck, and the better preserved is figured here. The species is probably new but its description must await additional material. Particularly conspicuous is the anterior glabellar tongue, which is quadrate, parallel sided, and steeply turned down frontally.

Remopleurides sp.

(Pl. 18, fig. 5)

1959*a*. *Remopleurides* aff. *burmeisteri* Bancroft: Dean, p. 207.

One flattened, incomplete cranidium from the Dufton Shales, Onnian Stage, *Onnia gracilis* Zone, at locality A. 12 in Pus Gill provides the only known record of the genus from the Onnian of the Cross Fell Inlier. Comparison with other species is difficult owing to the poor state of preservation, but the glabella lacks the glabellar furrows of *Remopleurides burmeisteri*, and the two are not now thought to be related. In south Shropshire *Remopleurides* appears rarely in the *Onnia gracilis* Zone and becomes more abundant in the succeeding *O. superba* Zone.

Remopleurides sp.

(Pl. 18, figs. 9, 11, 13)

1959*a*. *Remopleurides* sp. ind., Dean, p. 208.

Several fragments of *Remopleurides* have been collected from a thin band of sandy limestone within the highest beds of the Dufton Shales, Pusgillian Stage, at locality B. 25 in Swindale Beck. They comprise only flattened cranidia, with occasional thoracic segments and librigenae, but it seems unlikely that more than one species is represented.

The cranidia are too distorted for detailed comparison but bear a general resemblance to the cranidium of *Remopleurides colbii* Portlock (1843 : 254, pl. 1, figs. 1–6 ; pl. 24, fig. 10) from the Killey Bridge Beds of County Tyrone, Northern Ireland, a species redescribed by Whittington (1950 : 540, pl. 70, figs. 1, 2, 4, 5). Each of a group of three conjoined thoracic segments (Pl. 13, fig. 11) from Swindale Beck has an axial ring with a serrated posterior margin, a feature found not only in *R. colbii* but also in the Swedish species *R. validus*, described by Thorslund (1940 : 132, pl. 7, fig. 4) from the Lower Chasmops Limestone of the Lockne area. Three librigenae are known from the Pusgillian, one being figured here (Pl. 13, fig. 9). The librigenal spine is situated forwards from the genal angle, from which it is separated by what Warburg (1925 : 87) called a subgenal notch, a structure she described in *R. latus* var. *kullsbergensis* (1925 : 84, text-fig. 15). Subgenal notches are present in certain other species of *Remopleurides*, but do not occur in *R. colbii*.

IV. STRATIGRAPHICAL DISTRIBUTION AND RELATIONSHIPS OF THE TRILOBITES

Lithologically the Caradoc strata of the Cross Fell Inlier form what is essentially a succession of shales and mudstones, broken only by thin layers of impure, nodular limestone. Such a succession is in marked contrast with the, probably, shallower-water deposits of south Shropshire, and their thick development of arenaceous rocks. As might be expected, such differences in lithology are accompanied by variations in the composition of the shelly fauna, though it has generally proved possible to apply the faunal Stages of the type-succession to the Inlier.

In south Shropshire the local base of the Caradoc Series is usually formed by the Costonian Stage and falls within the *Nemagraptus gracilis* Zone, so that it may be equated with part of a profound and widespread marine transgression. Subsidence of the sea-floor probably continued through the whole of the time represented by the succeeding *Diplograptus multidens* Zone, believed to comprise the Harnagian and Soudleyan Stages, and may have been prolonged still further because the earliest-known Caradoc strata of the Cross Fell Inlier belong to the Lower Longvillian Substage and probably lie unconformably on the Borrowdale Volcanic Series, though an unfaulted junction of the two has not been found satisfactorily exposed.

The trilobites of the earlier Longvillian rocks in the Knock-Dufton and Roman Fell districts are neither abundant nor varied, comprising only a local species of *Proetidella*?, with occasional *Brongniartella* and *Broeggerolithus*, suggesting affinity with the northern part of the Inlier. The fauna of the Melmerby district is particularly characterized by an abundance of Trinucleidae, especially *Broeggerolithus nicholsoni* (Reed), accompanied by common *Kloucekia apiculata* (M'Coy), indicating an intimate connection with the faunas of the Drygill Shales of the northern Lake District and parts of North Wales, for example the Llanbedrog Mudstones. These two trilobites occur also in Shropshire, but in much reduced numbers. The genera *Chasmops*, *Conolichas*, *Illaenus* and *Toernquistia* at Melmerby suggest a connection with corresponding Scandinavian and Baltic faunas, whilst *Paracybeloides* occurs commonly in Scottish and North American Ordovician rocks, though it is known from stratigraphically early horizons in the Caradoc of North Wales.

In the Upper Longvillian of the Knock-Dufton district, *Brongniartella bisulcata* (M'Coy) is moderately common, as it is in south Shropshire, but its frequent Shropshire associate *Kloucekia apiculata* has not yet been found. Conversely, *Estoniops alifrons* (M'Coy) represents a group of phacopid trilobites which is widespread in the Baltic region and Scandinavia, as well as throughout much of North Wales, though unrecorded in Shropshire. Trinucleid trilobites have not been found in the Upper Longvillian rocks of the main part of the Inlier, and their absence has not been explained satisfactorily.

The trilobites of the Marshbrookian Stage are numerically abundant, though lacking in variety, and are generally comparable with those of Shropshire. *Brongniartella bisulcata* is moderately common and trinucleids, *Broeggerolithus* cf. *transiens* (Bancroft), fairly common. *Dindymene*, a European genus, is rare and has not yet been found in Shropshire, though it occurs also in the Upper Longvillian near Dufton, and in North Wales. A notable absentee from this horizon in the Cross Fell Inlier is *Chasmops*, a surprising fact in view of its abundance in Shropshire.

Owing to the lack of outcrops of Actonian strata in the Inlier the trilobites of this Stage are poorly known, but the assemblage of *Chasmops*, *Onnicalymene* and *Remopleurides* indicates connections with both Shropshire and Scandinavian faunas.

In the rocks of the Onnian Stage the resemblance between the fauna of the Dufton district and south Shropshire is most marked. *Onnia gracilis* (Bancroft), a species found also in North Wales, occurs in the Onny Valley and at Pus Gill, accompanied at both places by *Lonchodomas pennatus* (La Touche) and *Onnicalymene onniensis* (Shirley). In the succeeding zone the well-known Shropshire species *Onnia superba*

(Bancroft) is represented by a local subspecies *O. superba pusgillensis*. An interesting feature of the Onnian fauna at Cross Fell is the appearance of such genera as *Atractopyge*, *Calyptaulax*, *Pseudosphaerexochus* and *Tretaspis*, marking an influx from the Scandinavian area which assumed greater proportions during the succeeding Pusgillian Stage.

The Pusgillian has at various times been assigned to the Ashgill Series, but is now regarded as the topmost subdivision of the Caradoc Series. Trinucleid trilobites are abundant at this horizon, but the genus *Onnia*, so characteristic of the Onnian is absent and the family is represented only by *Tretaspis*. The latter genus is represented by several species or subspecies, all of which indicate close affinities with corresponding faunas in southern Norway and Sweden. Most of, if not all, the other trilobites in the Pusgillian are members of genera which have generally been thought to be more characteristic of Ashgill strata. The trilobite faunas of the Ashgill Series exhibit a uniformity and widespread distribution which are unknown in those of the Caradoc Series, and several genera and species are common to Scotland, the Anglo-Welsh area, Scandinavia and eastern Europe. The Onnian and Pusgillian strata of the Cross Fell Inlier are of particular interest because they demonstrate that the Ashgill elements invaded the Anglo-Welsh area at a relatively early date, after which there was a progressive increase in their numbers.

V. REFERENCES

BANCROFT, B. B. 1929. Some new species of *Cryptolithus* (*s.l.*), from the Upper Ordovician. *Mem. Proc. Manchr Lit. Phil. Soc.*, **73** : 67–98, pls. 1, 2.

—— 1933. *Correlation Tables of the Stages Costonian–Onnian in England and Wales.* 4 pp., 3 tables. Blakeney, Glos. (Privately printed.)

—— 1949. Upper Ordovician trilobites of zonal value in South-east Shropshire. *Proc. Roy. Soc.*, London (B) **136** : 291–315, pls. 9–11. (Edited by A. Lamont.)

BARRANDE, J. 1852. *Systême silurien du centre de la Bohême. 1ère partie. Recherches paléontologiques.* xxx + 935 pp., Atlas of 51 plates. Prague & Paris.

BASSLER, R. S. 1915. Bibliographic index of American Ordovician and Silurian fossils. *Bull. U.S. Nat. Mus.*, Washington, **92** : 1–1521, 4 pls.

COOPER, B. N. 1953. Trilobites from the Lower Champlainian Formations of the Appalachian Valley. *Mem. Geol. Soc. Amer.*, Baltimore, **55** : i–v, 1–69, pls. 1–19.

COOPER, G. A. 1930. Upper Ordovician and Lower Devonian stratigraphy and paleontology of Percé, Quebec. Part II. New species from the Upper Ordovician of Percé. *Amer. J. Sci.*, New Haven, **20** : 365–392, pls. 4, 5.

DALMAN, J. W. 1828. Nya Svenska Palaeader. *Årsberättelse om nyare Zoologiska Arbeten och Upptäckter till Kongl. Vetenskaps-Academien* : 134–135. Stockholm.

DEAN, W. T. 1958. The faunal succession of the Caradoc Series of South Shropshire. *Bull. Brit. Mus.* (*Nat. Hist.*) *Geol.*, London, **3** : 191–231, pls. 24–26.

—— 1959. *Duftonia*, a new trilobite genus from the Ordovician of England and Wales. *Palaeontology*, London, **2** : 143–149, pl. 19.

—— 1959*a*. The stratigraphy of the Caradoc Series in the Cross Fell Inlier. *Proc. Yorks. Geol. Soc.*, Hull, **32** : 185–228, 6 figs.

—— 1960. The Ordovician trilobite faunas of South Shropshire, I. *Bull. Brit. Mus.* (*Nat. Hist.*) *Geol.*, London, **4** : 71–143, pls. 11–19.

—— 1961. Trinucleid trilobites from the higher Dufton Shales of the Caradoc Series in the Cross Fell Inlier. *Proc. Yorks. Geol. Soc.*, Hull, **33** : 119–134, pls. 7–9.

—— 1961*a*. The Ordovician trilobite faunas of South Shropshire, II. *Bull. Brit. Mus.* (*Nat. Hist.*) *Geol.*, London, **5** : 311--358, pls. 49–55.

DELO, D. M. 1935. A revision of the phacopid trilobites. *J. Paleont.*, Menasha, **9** : 402–420, 45 figs.

ELLES, G. L. 1922. The Bala country : its structure and rock-succession. *Quart. J. Geol. Soc. Lond.*, **78** : 132–175, pl. 2.

EMMRICH, H. F. 1844. *Zur Naturgeschichte der Trilobiten.* 28 pp., 1 pl. Meinigen.

FISHER, D. W. 1957. Mohawkian (Middle Ordovician) biostratigraphy of the Wells Outlier, Hamilton County, New York *Bull. New York State Mus.*, Albany, **359** : 1–33, 6 pls.

FOERSTE, A. F. 1910. Preliminary notes on Cincinnatian and Lexington fossils of Ohio, Indiana, Kentucky and Tennessee. *Bull. Sci. Lab. Denison Univ.*, Granville, **16** : 15–87, pls. 1–7.

—— 1919. Silurian fossils from Ohio, with notes on related species from other horizons. *Ohio Journ. Sci.*, Columbus, **19** : 367–404, pls. 16–19.

GREEN, J. 1832. *A monograph of the trilobites of North America : with coloured models of the species.* 94 pp., 10 figs. Philadelphia.

GÜRICH, G. 1901. Ueber eine neue *Lichas*-Art aus dem Devon von Neu-Süd-Wales und über die Gattung *Lichas* überhaupt. *N. Jb. Min. Geol. Paläont.*, Stuttgart, **14** : 519–539, pls. 18–20.

HARKNESS, R. & NICHOLSON, H. A. 1877. The strata and their fossil contents between the Borrowdale Series of the north of England and the Coniston Flags. *Quart. J. Geol. Soc. Lond.*, **33** : 461–484, 4 figs.

HARPER, J. C. 1947. The Caradoc fauna of Ynys Galed, Caernarvonshire. *Ann. Mag. Nat. Hist.*, London (11) **14** : 153–175, pls. 6, 7.

—— 1956. The Ordovician succession near Llanystwmdwy, Caernarvonshire. *Liv. Manchr. Geol. J.*, Birkenhead, **1** : 385 393, 1 fig.

HAWLE, I. & CORDA, A. J. C. 1847. *Prodrom einer monographie der böhmischen trilobiten.* 176 pp., 7 pls. Prague.

HOLM, G. 1886. Revision der ostbaltischen silurischen Trilobiten. Abh. III. Die ostbaltischen Illaeniden. *Mém. Acad. Imp. Sci. St. Pétersb.*, **33**, 8 : 1–173, pls. 1–12.

HUPÉ, P. 1955. Classification des Trilobites. *Ann. Paléont.*, Paris, **41** : 111–345, figs. 93, 247.

JAANUSSON, V. 1953. Über die Fauna des oberordovizischen Slandrom-Kalksteines im Siljan-Gebiet, Dalarna. *Geol. Fören. Stockh. Förh.*, **75** : 97–105, 4 figs.

—— 1954. Zur morphologie und taxonomie der Illaeniden. *Ark. Min. geol.*, Stockholm, **1** : 545–583, 3 pls.

KEGEL, W. 1937. Über obersilurische Trilobiten aus dem Harz und dem Rheinischen Schiefergebirge. *Jb. preuss. geol. Landesanst.*, Berlin, **48** : 616–647, pls. 31, 32.

KIELAN, Z. 1959. Upper Ordovician trilobites from Poland and some related forms from Bohemia and Scandinavia. *Pal. Polonica*, Warsaw, **11** : vi + 198 pp., 36 pls.

KING, W. B. R. 1923. The Upper Ordovician rocks of the south-western Berwyn Hills. *Quart. J. Geol. Soc. Lond.*, **79** : 487–507, pl. 26.

LAMONT, A. 1941. Trinucleidae in Eire. *Ann. Mag. Nat. Hist.*, London (11) **8** : 438–469, pl. 5.

—— 1946. B. B. Bancroft's geological work. 1. Caradocian lavas and sediments in the Capel Curig district, Caernarvonshire. *Quarry Manager's J.*, Mexborough, **30** : 235–239, figs. 1–5.

—— 1948. B. B. Bancroft's geological work. 2. Upper Ordovician of the Cross Fell Inlier. *Quarry Manager's J.*, Mexborough, **31** : 416–418, 466–469, 1 pl.

LA TOUCHE, J. D. 1884. *A Handbook of the Geology of Shropshire.* 99 pp., 22 pls. London & Shrewsbury.

MÄNNIL, R. 1958. *Estoniops*—a new genus of Phacopidae (Trilobita). *Eesti NSV Teaduste Akad Toimetised*, Tallin, **6** : 385–388, 1 pl. (In Russian with Estonian and English summaries.)

MARR, J. E. 1892. The Coniston Limestone Series. *Geol. Mag. Lond.*, **9** : 97–110.

M'COY, F. 1846. *A synopsis of the Silurian fossils of Ireland.* 68 pp., 4 pls. Dublin.

M'Coy, F. 1849. On the classification of some British fossil Crustacea, with notices of some new forms in the University collection at Cambridge. *Ann. Mag. Nat. Hist.*, London (2) **4** : 161–179, 330–335, 392–414.

Moore, R. C. 1959. *Treatise on Invertebrate Paleontology. Part O. Arthropoda* 1. xix + 560 pp., 415 figs. Kansas & Connecticut.

Nicholson, H. A. & Etheridge, R. 1878. *A monograph of the Silurian fossils of the Girvan district in Ayrshire.* ix + 341 pp., 24 pls. Edinburgh & London.

Nicholson, H. A. & Marr, J. E. 1891. The Cross Fell Inlier. *Quart. J. Geol. Soc. Lond.*, **47** : 500–512, pl. 17.

Öpik, A. A. 1937. Trilobiten aus Estland. *Acta Univ. dorpat. (tartu), A*, **32** : 1–163, pls. 1–26.

Phleger, F. B. 1937. Species and geographic distribution of the Lichadacea. *Amer. Midl. Nat.*, Notre Dame, **18** : 1085–1092.

Portlock, J. E. 1843. *Report on the geology of the county of Londonderry and of parts of Tyrone and Fermanagh.* xxxi + 784 pp., pls. 1–38, A–I. Dublin & London.

Přibyl, A. 1953. Seznam českých trilobitových rodů (Index of trilobite genera in Bohemia). *Knihovna Ústř. úst. geol.*, Prague, **25** : 1–80. (In Czech, Russian and English.)

Rafinesque, C. S. 1832. On the genera of fossil Trilobites or Glomerites of North America. *Atlantic J. & Friend of Knowledge*, Philadelphia, **1** : 71–73.

Raymond, P. E. 1925. Some trilobites of the lower Middle Ordovician of eastern North America. *Bull. Mus. Comp. Zool. Harvard*, Cambridge, **67** : 1–180, pls. 1–10.

Reed, F. R. C. 1896. The fauna of the Keisley Limestone, Part I. *Quart. J. Geol. Soc. Lond.*, **52** : 407–437, pls. 20, 21.

—— 1896*a*. Notes on the evolution of the genus *Cheirurus*. *Geol. Mag. Lond.* (4) **3** : 117–123, 161–167.

—— 1904. The Lower Palaeozoic Trilobites of the Girvan District, Ayrshire, **2** : 49–96, pls. 7–13. *Palaeontogr. Soc.* [*Monogr.*], London.

—— 1905. New fossils from the Haverfordwest District. III. *Geol. Mag. Lond.* (5) **2** : 97–104, pl. 4.

—— 1905*a*. The classification of the Phacopidae. *Geol. Mag. Lond.* (**5**) **2** : 172–178, 224–228.

—— 1906. The Lower Palaeozoic Trilobites of the Girvan District, Ayrshire, **3** : 97–186, pls. 14–20. *Palaeontogr. Soc.* [*Monogr.*], London.

—— 1907. A new species of *Lichas*. *Geol. Mag. Lond.* (5) **4** : 396–400, pl. 17.

—— 1910. New fossils from the Dufton Shales. *Geol. Mag. Lond.* (5) **7** : 211–220, 294–299, pls. 16, 17, 23, 24.

—— 1912. Notes on the genus *Trinucleus*. *Geol. Mag. Lond.* (5) **9** : 346–353, 385–394, pls. 18, 19.

—— 1914. Notes on the genus *Trinucleus*.—Part III. *Geol Mag. Lond.* (6) **1** : 349–359, pls. 28, 29.

—— 1914*a*. The Lower Palaeozoic Trilobites of the Girvan District, Ayrshire, Supplement : 1–56, pls. 1–8. *Palaeontogr. Soc.* [*Monogr.*], London.

—— 1918. Notes on the genus *Homalonotus*. *Geol. Mag. Lond.* (6) **5** : 263–276, 314–327.

—— 1931. The Lower Palaeozoic Trilobites of the Girvan District, Ayrshire, Supplement No. **2** : 1–30. *Palaeontogr. Soc.* [*Monogr.*], London.

—— 1932. Notes on two species of the genus *Ampyx*. *Geol. Mag. Lond.*, **69** : 205–209, pl. 11.

—— 1945. Notes on some Ordovician Brachiopods and a Trilobite from the Balclatchie Beds of Girvan. *Ann. Mag. Nat. Hist.*, London (11) **12** : 309–316, 1 pl.

Richter, R. 1940. Referata, Arthropoda. *N. Jb. Min., Geol., Paläont.*, Stuttgart, **3** : 1030–1031.

Richter, R. & E. 1917. Über die Einteilung der Familie Acidaspidae und über einige ihrer devonischen Vertreter. *Zbl. Min. Geol. Paläont.*, Stuttgart, 462–472, 10 figs.

—— 1926. Die Trilobiten des Oberdevons, Beiträge zur Kenntnis devonischer Trilobiten, 4. *Abh. preuss. geol. Landesanst.*, Berlin, **99** : 1–314, pls. 1–12.

Salter, J. W. 1852. *Appendix A*, to Sedgwick & M'Coy, *A synopsis of the classification of the British Palaeozoic rocks with a systematic description of the British Palaeozoic fossils in the geological museum of the University of Cambridge.* i–viii. London & Cambridge.

SALTER, J. W. 1853. Figures and descriptions illustrative of British organic remains. *Mem. Geol. Surv. Gt. Britain*, London, **7** : 78 pp., pls. 1–10.

—— 1857. On two Silurian species of *Acidaspis* from Shropshire. *Quart. J. Geol. Soc. Lond.*, **13** : 210–211, pl. 6.

—— 1864. A Monograph of the British Trilobites from the Cambrian, Silurian, and Devonian formations, **1** : 1–80, pls. 1–6. *Palaeontogr. Soc.* [*Monogr.*], London.

—— 1873. *A Catalogue of the collection of Cambrian and Silurian fossils contained in the geological museum of the University of Cambridge.* xlviii + 204 pp. Cambridge.

SCHMIDT, F. 1881. Revision der ostbaltischen silurischen Trilobiten nebst geognostischer Übersicht des ostbaltischen Silurgebiets, Abtheilung 1, Phacopiden, Cheiruriden und Encrinuriden. *Mém. Acad. Imp. Sci. St. Pétersb.* (7) **30** : i–iv, 1–237, pls. 1–16.

—— 1907. Revision der Ostbaltischen Silurischen Trilobiten. Abtheilung 6. *Mém. Acad. Imp. Sci. St. Pétersb.* (8) **20** : i–xv, 1–104, pls. 1–3.

SEDGWICK, A. & M'COY, F. 1851. *A synopsis of the classification of the British Palaeozoic rocks, with a systematic description of the British Palaeozoic fossils in the geological museum of the University of Cambridge.* Fasc. I. iv + 184 pp., 11 pls. London & Cambridge.

SHIRLEY, J. 1931. A redescription of the known British Ordovician species of *Calymene* (s.l.). *Mem. Manchr. Lit. Phil. Soc.*, **75** : 1–35, 2 pls.

—— 1936. Some British trilobites of the Family Calymenidae. *Quart. J. Geol Soc. Lond.*, **92** : 384–422, pls. 29–31.

SHOTTON, F. W. 1935. The stratigraphy and tectonics of the Cross Fell Inlier. *Quart. J. Geol. Soc. Lond.*, **91** : 639–704, pl. 39.

SIMPSON, G. B. 1890. Descriptions of new species of fossils from the Clinton, Lower Helderberg, Chemung and Waverly groups, found in the collections of the Geological Survey of Pennsylvania. *Trans. Amer. Phil. Soc.*, Philadelphia, **16** : 435–460, 31 figs.

STETSON, H. C. 1927. The distribution and relationships of the Trinucleidae. *Bull. Mus. Comp. Zool. Harvard*, Cambridge, **68** : 87–104, 1 pl.

STØRMER, L. 1940. Early descriptions of Norwegian trilobites. The type specimens of C. Boeck, M. Sars and M. Esmark. *Norsk. geol. tidsskr.*, Oslo, **20** : 113–151, pls. 1–3.

—— 1945. Remarks on the *Tretaspis* (*Trinucleus*) Shales of Hadeland, with description of trilobite faunas. *Norsk. geol. tidsskr.*, Oslo, **25** : 379–426, pls. 1–4.

STUBBLEFIELD, C· J. 1928. A new trilobite, *Acidaspis* (*Pseudomonaspis*) *magnospina*, from the Coniston Limestone. *Ann. Mag. Nat. Hist.*, London (10) **1** : 427–433, pl. 14.

STUMM, E. C. & KAUFMANN, E. G. 1958. Calymenid trilobites from the Ordovician rocks of Michigan. *J. Paleont.*, Tulsa, **32** : 943–960, pls. 123, 124.

TEMPLE, J. T. 1952. A revision of the trilobite *Dalmanitina mucronata* (Brongniart) and related species. *Lunds Univ. Årsskr.* (N.F., 2) **48** : 1–33, pls. 1–4.

THORSLUND, P. 1940. On the Chasmops Series of Jemtland and Södermanland (Tvären). *Sverig. Geol. Unders. Afh.*, Stockholm (C) **436** : 1–191, pls. 1–15.

TRIPP, R. P. 1954. Caradocian Trilobites from mudstones at Craighead Quarry, near Girvan, Ayrshire. *Trans. Roy. Soc. Edin.*, **62** : 655–693, pls. 1–4.

—— 1957. The trilobite *Encrinurus multisegmentatus* (Portlock) and allied Middle and Upper Ordovician species. *Palaeontology*, London, **1** : 60–72, pls. 11, 12.

—— 1958. Stratigraphical and geographical distribution of the named species of the trilobite Superfamily Lichacea. *J. Paleont.*, Tulsa, **32** : 574–582, pl. 85.

TROEDSSON, G. 1929. On the Middle and Upper Ordovician faunas of Northern Greenland, Pt. II. *Medd. Grønland*, Kjøbenhavn, **72** : 1–197, pls. 1–56.

VOGDES, A. W. 1890. A bibliography of Paleozoic Crustacea from 1698 to 1889 including a list of North American species and a systematic arrangement of genera. *Bull. U.S. Geol. Surv.*, Washington, **63** : 1–177.

WARBURG, E. 1939. The Swedish Ordovician and Lower Silurian Lichidae. *K. svenska VetenskAkad. Handl.*, Stockholm, **17** (4) : 1–162, pls. 1–14.

WEDD, C. B., SMITH, B., KING, W. B. R. & WRAY, D. A. 1929. The country around Oswestry. *Mem. Geol. Surv.*, London. x + 234 pp., 4 pls.

WHITCOMB, L. 1930. New information on *Homalonotus trentonensis*. *Bull. Geol. Soc. Amer.*, New York, **41** : 341–350, pls. 5, 6.

WHITTARD, W. F. 1955. The Ordovician trilobites of the Shelve Inlier, West Shropshire, **1** : 1–40, pls. 1–4. *Palaeontogr. Soc.* [*Monogr.*], London.

—— 1960. The Ordovician trilobites of the Shelve Inlier, West Shropshire, **4** : 117–162, pls. 16–21. *Palaeontogr. Soc.* [*Monogr.*], London.

—— 1961. The Ordovician trilobites of the Shelve Inlier, West Shropshire, **5** : 163–196, pls. 22–25. *Palaeontogr. Soc.* [*Monogr.*], London.

—— 1961*a*. The Ordovician trilobites of the Shelve Inlier, West Shropshire, **6** : 197–228, pls. 26–30. *Palaeontogr. Soc.* [*Monogr.*], London.

WHITTINGTON, H. B. 1938. The geology of the country around Llansantffraid ym Mechain, Montgomeryshire. *Quart. J. Geol. Soc. Lond.*, **94** : 423–457, pls. 38, 39.

—— 1940. On some Trinucleidae described by Joachim Barrande. *Amer. J. Sci.*, Washington, **238** : 241–259, pls. 1–4.

—— 1950. Sixteen Ordovician genotype trilobites. *J. Paleont.*, Tulsa, **24** : 531–565, pls. 68–75.

WHITTINGTON, H. B. & EVITT, W. R. 1954. Silicified Middle Ordovician trilobites. *Mem. Geol. Soc. Amer.*, Baltimore, **59** : 1–137, pls. 1–33.

WHITTINGTON, H. B. & WILLIAMS, A. 1955. The fauna of the Derfel Limestone of the Arenig district, North Wales. *Philos. Trans.*, London (B) **238** : 397–430, pls. 38–40.

WIGAND, G. 1888. Ueber die Trilobiten der Silurischen Geschiebe in Mecklenburg. *Z. dtsch. geol. Ges.*, Berlin, **40** : 39–101, pls. 6–10.

WIMAN, C. 1908. Studien über das Nordbaltische Silurgebiete. *Bull. Geol. Inst. Univ. Uppsala*, **8** : 73–168, pls. 5–8.

WOODS, H. 1891. *Catalogue of the type fossils in the Woodwardian Museum, Cambridge.* xiv + 180 pp. Cambridge.

27 AUG 67

PLATES

Most of the type and figured specimens are in the collections of the British Museum (Natural History), London, and bear numbers with the prefix In. Other numbers with the prefix A. denote specimens in the Sedgwick Museum, Cambridge, whilst one specimen, GSM 19165 (Pl. 12, fig. 2), is in the Geological Survey & Museum, London. The locality numbers refer to the sketch-maps elsewhere in this paper. All the photographs are by the writer, the specimens having been whitened with ammonium chloride before photographing.

PLATE 6

Lonchodomas pennatus (La Touche) . . . . . p. 78

Dufton Shales, Pusgillian Stage, Swindale Beck, locality B.25.

FIG. 1. Internal mould of cranidium showing upturned frontal spine. In. 49933. ×2.

FIG. 3. Internal mould of incomplete cranidium. In. 49934. ×2.

FIG. 4. Internal mould of flattened cranidium showing hypostomal pits. In. 49936. ×2.

FIG. 5. Internal moulds of two small pygidia, probably immature. In. 49931. ×2·75.

Dufton Shales, Onnian Stage, *Onnia gracilis* Zone, Pus Gill, locality A.8.

FIG. 9. Internal mould of cranidium. In. 49979. ×2·25.

Horizon as for Fig. 9, Pus Gill, locality A.14.

FIG. 12. Internal mould of pygidium. In. 49926. ×2·5.

Lonchodomas swindalensis sp. nov. . . . . . p. 72

Dufton Shales, Upper Longvillian Substage, *Kjaerina typa* Zone, Swindale Beck, locality B.6.

FIG. 2. Cranidium with part of test preserved. Holotype. In. 49968. ×2·25.

Horizon as for Fig. 2, Swindale Beck, locality B.5.

FIG. 6. Latex cast from external mould of pygidium. Paratype. In. 49967. ×4·5.

FIG. 8. Latex cast from external mould of cranidium. Paratype. In. 49946. ×3.

Broeggerolithus nicholsoni (Reed) . . . . . p. 79

Probably Upper Melmerby Beds, Upper Longvillian Substage, Alston Road, locality A.

FIG. 7. Internal mould of cranidium. In. 52570. ×4.

Broeggerolithus melmerbiensis sp. nov. . . . . . p. 81

Horizon and locality as for Fig. 7.

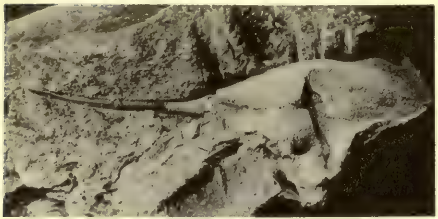
FIGS. 10, 13. Almost complete cranidium with three attached thoracic segments. Holotype. In. 52558. ×1·75.

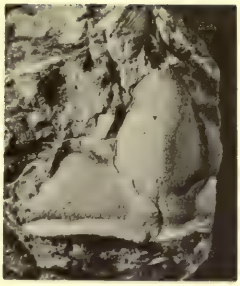
Broeggerolithus cf. *nicholsoni* (Reed) . . . . . p. 80

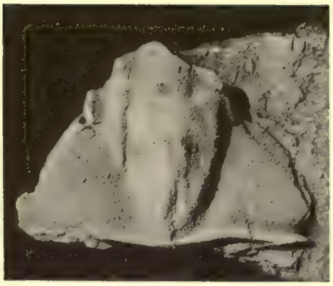
Corona Beds, Lower Longvillian Substage, *Bancroftina typa* Zone, Harthwaite Sike, locality E.3.

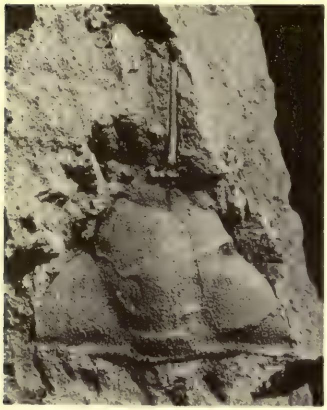
FIG. 11. Latex cast from external mould of fragmentary cephalic fringe. In. 54640*b*. ×2·5.

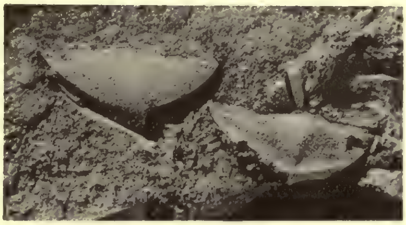
FIG. 14. Latex cast from external mould of incomplete pygidium. In. 54643. ×3.

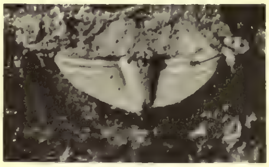

1

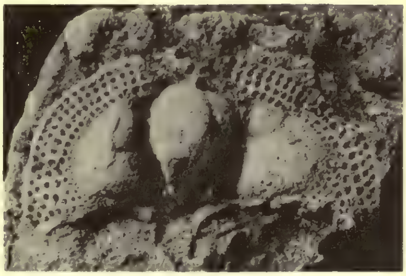

2

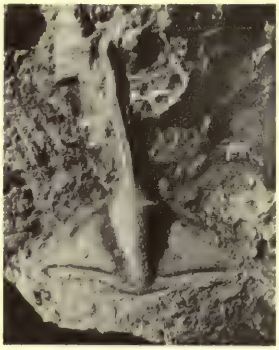

3

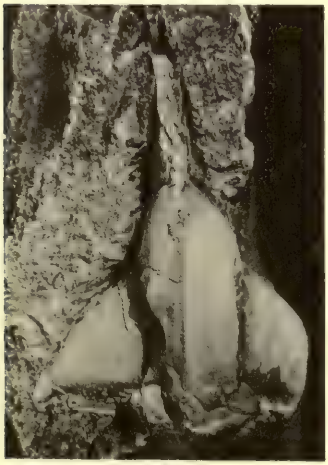

4

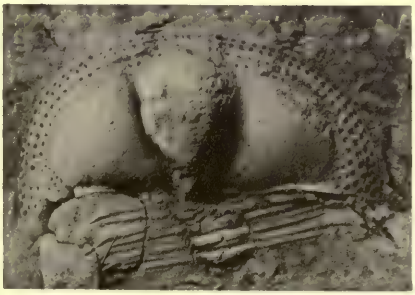

5

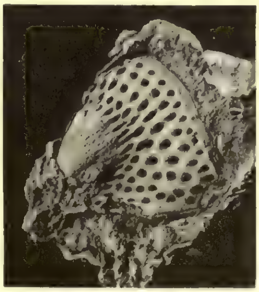

6

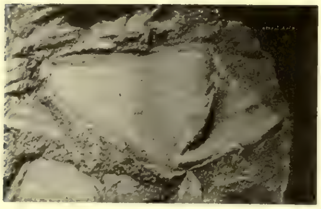

7

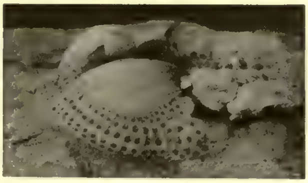

8

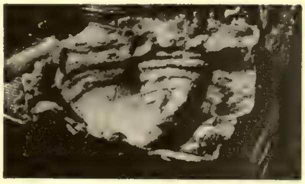

9


10


11


12


13


14

LONCHODOMAS, BROEGGEROLITHUS

PLATE 7

Broeggerolithus nicholsoni (Reed) . . . . p. 79

Lower Melmerby Beds, Lower Longvillian Substage, probably Alston Road, locality J.

FIGS. 1, 7. Almost complete cephalon. Paratype. A. 29609. ×2·8.

FIG. 2. Internal mould of pygidium. Paratype. A. 29615. ×3.

FIG. 4. Internal mould of almost complete exoskeleton. A. 29946*a*. ×1·8.

FIG. 5. Fragmentary cranidium. Paratype. A. 29611. ×2·8.

FIGS. 6, 9. Almost complete cranidium. Lectotype. A. 29613. ×2·5.

FIG. 8. External mould of fragmentary cranidium. Paratype. A. 29612. ×2·8.

FIG. 10. Almost complete cranidium. Paratype. A. 29610. ×2·8.

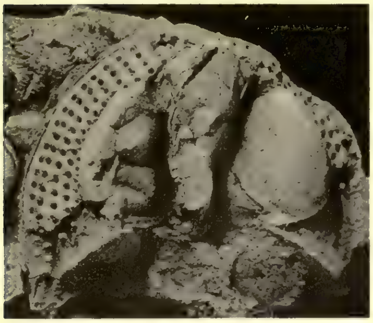
Probably Upper Melmerby Beds, Alston Road, locality uncertain.

FIG. 11. Cephalon preserved partly as an internal, partly as an external mould. Paratype. A. 29614. ×2·8.

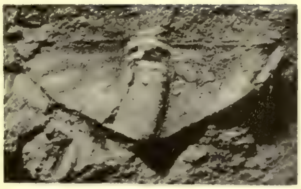
Probably Upper Melmerby Beds, Upper Longvillian Substage, Alston Road, locality A

FIG. 3. External mould of cephalic fragment showing reticulate surface of cheek-lobe. In. 52567. ×4.

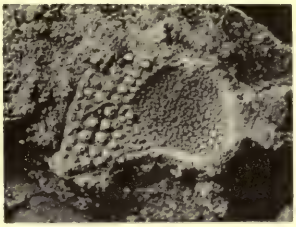
FIG. 12. External mould of underside of fringe showing pits and librigenal spine. In. 52576. ×3·5.



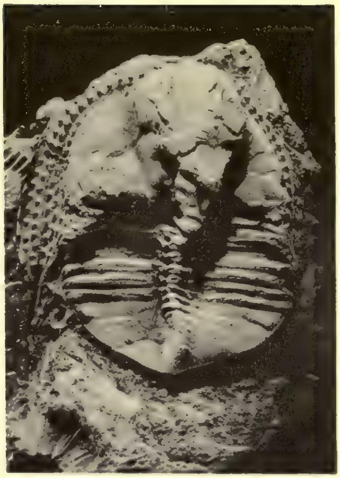
1



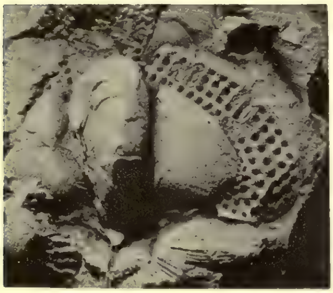
2



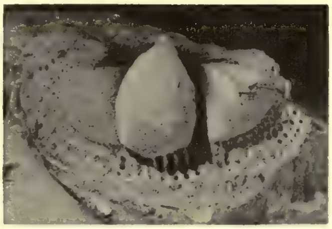
3



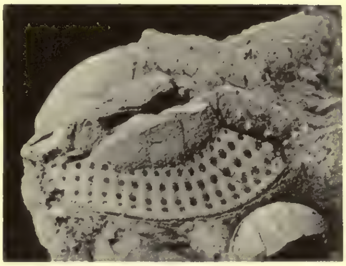
4



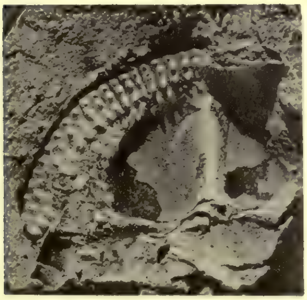
5



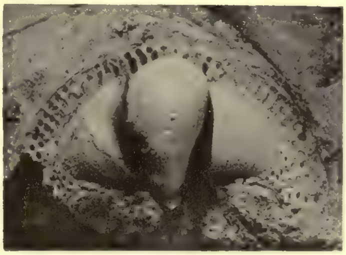
6



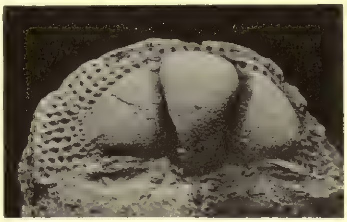
7



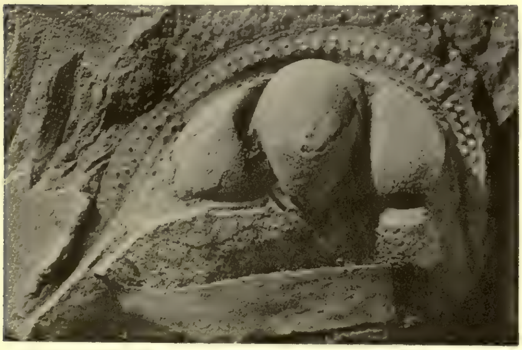
8



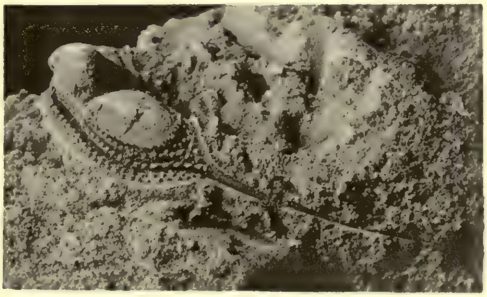
9



10



11



12

BROEGGEROLITHUS

PLATE 8

Broeggerolithus cf. *transiens* (Bancroft) . . . . p. 82

Dufton Shales, Marshbrookian Stage, probably topmost third, Swindale Beck, locality B.16.

FIG. 1. Internal mould of cranidium. In. 50216. ×2·2.

FIG. 6. Internal mould of underside of fringe. In. 50215. ×2.

Horizon as for Fig. 1. Swindale Beck, locality B. 11.

FIG. 3. Internal mould of fragmentary cephalon showing genal angle. In. 50244. ×2·75.

Horizon as for Fig. 1. Swindale Beck, locality B. 14.

FIG. 4. Internal mould of slightly distorted pygidium. In. 49957. ×2·5.

FIG. 8. Internal mould of fragmentary cranidium showing development of I_3. In. 50190. ×2.

Horizon as for Fig. 1. Harthwaite Sike, locality E. 8.

FIG. 11. Internal mould of small cranidium. In. 51853. ×3·5.

Broeggerolithus sp. . . . . . . p. 83

Horizon and locality as for Fig. 4.

FIG. 2. Latex cast from external mould of fragmentary cranidium. In. 50222. ×2.

Onnia gracilis (Bancroft) . . . . . . p. 84

Dufton Shales, Onnian Stage, Pus Gill, locality A.4.

FIG. 12. Internal mould of cranidium showing pitting of fringe. In. 50001. ×3.

FIG. 13. Damaged, almost complete specimen showing pygidium and impression of underside of fringe. In. 49948. ×2·5.

Onnia superba (Bancroft) *pusgillensis* Dean . . . . p. 84

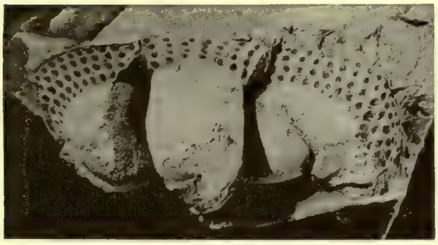
Dufton Shales, Onnian Stage, *Onnia superba* Zone, Pus Gill, locality A. 5.

FIG. 5. Internal mould of incomplete cranidium. Paratype. In. 50008. ×1·5.

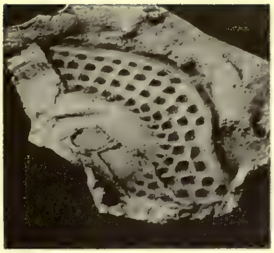
FIG 7. Fragmentary cranidium, an internal mould, accompanied by external mould of *Tretaspis*. In. 50003. ×1·5.

FIG. 9. Latex cast from external mould of two incomplete cranidia. Paratype. In. 50005. ×2.

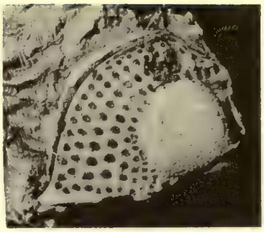
FIG. 10. Internal mould of pygidium. In. 50013. ×2·25.



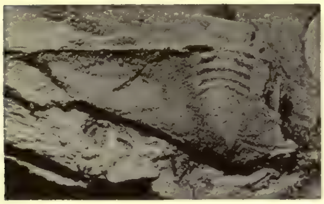
1



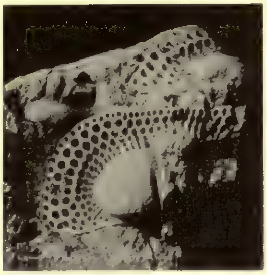
2



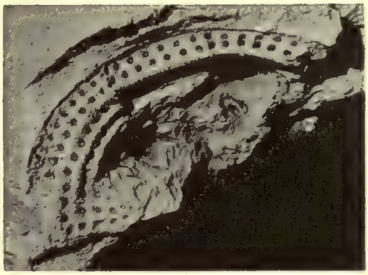
3



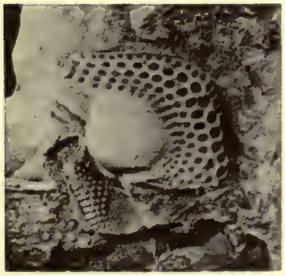
4



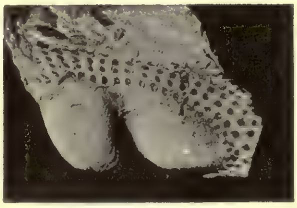
5



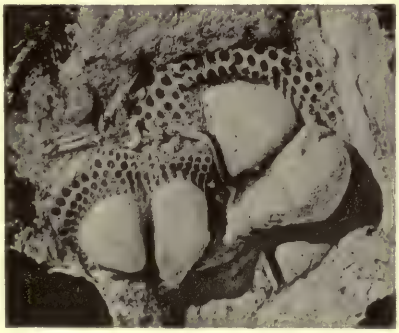
6



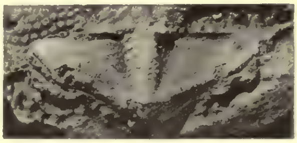
7



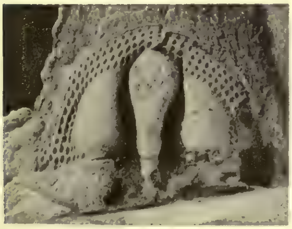
8



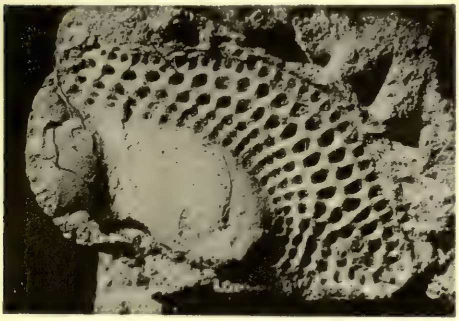
9



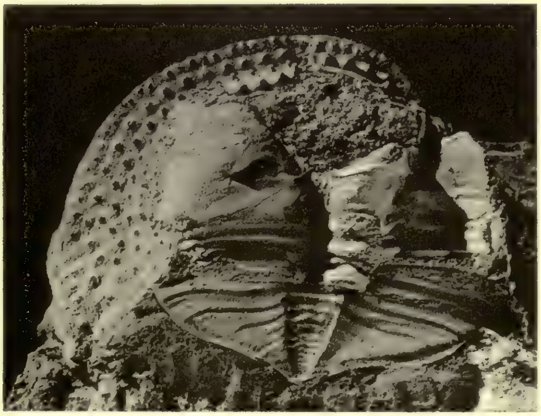
10



11



12



13

BROEGGEROLITHUS, ONNIA

PLATE 9

Tretaspis kiaeri (Størmer) *duftonensis* Dean . . . p. 86

Dufton Shales, Pusgillian Stage, Pus Gill, locality A. 27.

FIG. 1. Internal mould of almost complete individual showing median and lateral ocelli, thorax and pygidium. Holotype. In. 50020*a*. ×3.

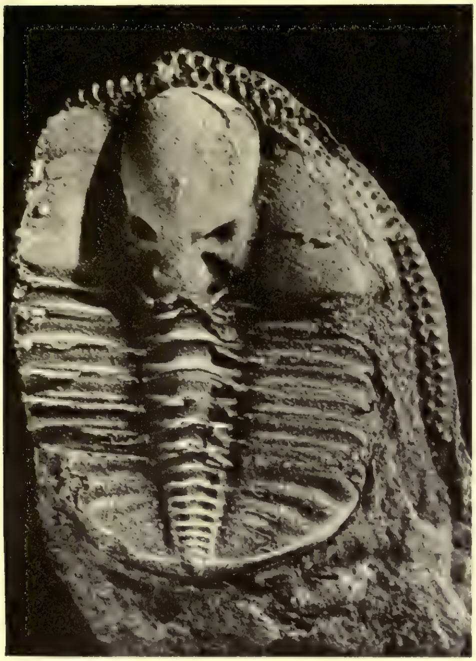
FIGS. 5–7. Latex cast from external mould of same specimen, showing surface of thorax and pygidium, reticulation of glabella, and fringe profile. In. 50020*b*. Figs. 5, 7, ×4. Fig. 6, ×3.

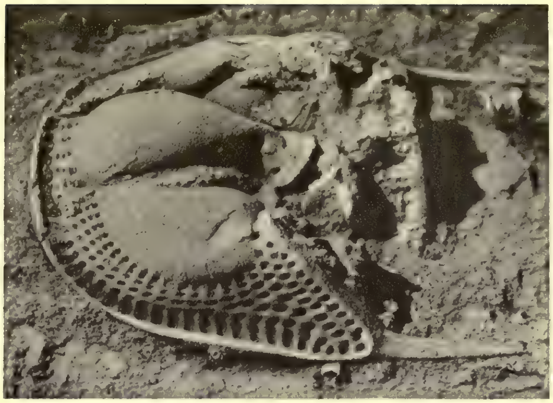
Tretaspis kiaeri (Størmer) *radialis* Lamont . . . p. 86

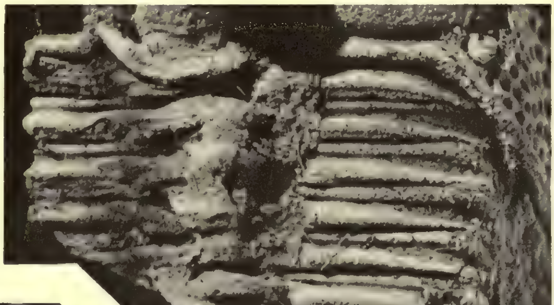
Horizon as for Fig. 1. Swindale Beck, locality B. 25.

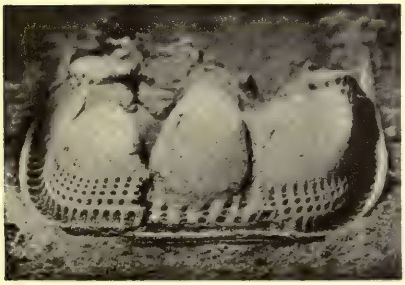
FIGS. 2, 3. Latex cast from external mould of cephalon, illustrating pitting of fringe, marginal suture, and grooved librigenal spines. In. 50045*b*. ×2·5.

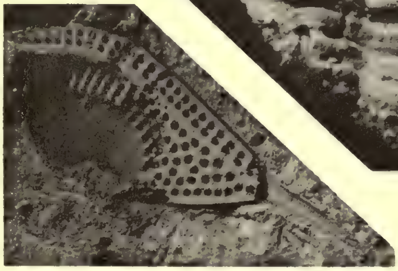
FIG. 4. Underside of fringe preserved as internal mould showing development of girder. In. 50052. ×2·5.

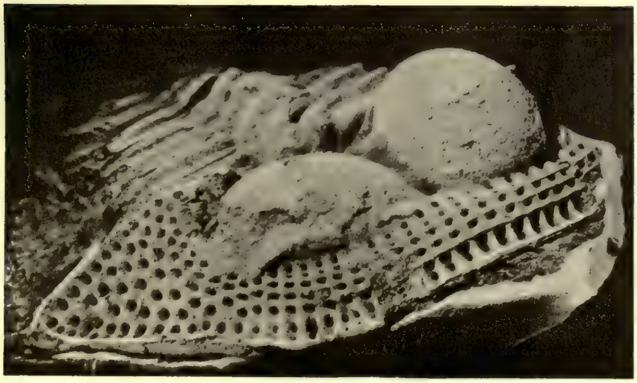

1

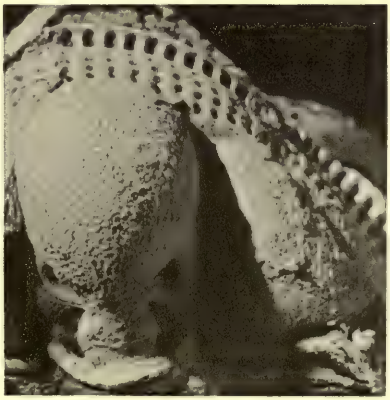

2


5


3


4


6


7

TRETASPIS

PLATE 10

Tretaspis convergens Dean . . . . . p. 85

Dufton Shales, Pusgillian Stage, Swindale Beck, locality B.25.

FIG. 1. Latex cast from external mould showing reticulation of cephalon. Holotype In. 50059*b*. ×3.

FIGS. 3, 5. Internal mould of same specimen. In. 50059*a*. ×2·5.

FIG. 2. Internal mould of part of cephalic fringe. Paratype. In. 50037.

Tretaspis cf. *ceriodes* (Angelin) *donsi* Størmer . . . p. 85

Dufton Shales, Onnian Stage, *Onnia superba* Zone, Pus Gill, locality A. 5.

FIGS. 4, 8. Latex cast from external mould of cephalon to show fringe and surface of glabella and cheek-lobes. In. 50018*b*. ×3.

Dufton Shales, Onnian Stage, *Onnia gracilis* Zone, Pus Gill, locality A. 13.

FIG. 6. Latex cast from external mould of fragment of fringe. In. 50096. ×3·5.

Pseudosphaerexochus cf. *octolobatus* (M'Coy) . . . p. 87

Horizon as for Fig. 1, Pus Gill, locality A. 6.

FIG. 7. Internal mould of incomplete pygidium. In. 49816. ×2·25.

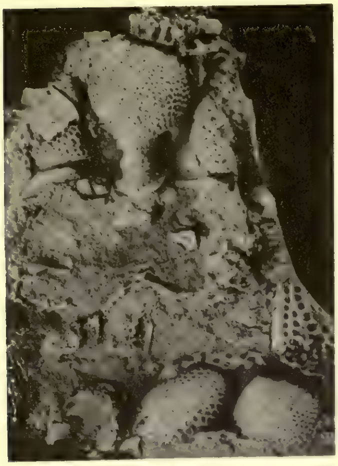
Horizon and locality as for Fig. 1.

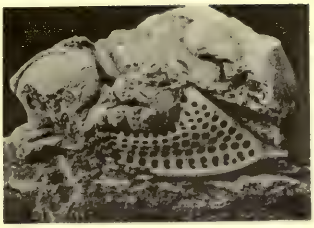
FIGS. 9, 10. Internal mould of cranidium. In. 49803. ×3·25.

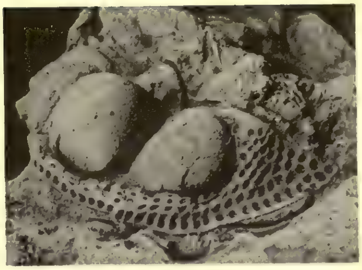
Horizon as for Fig. 1, Pus Gill, locality A. 22.

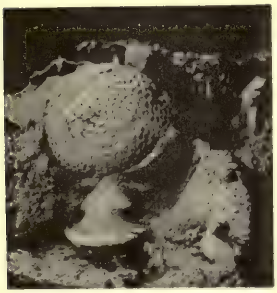
FIG. 11. Internal mould of incomplete cranidium. In. 49817*a*. ×1·75.

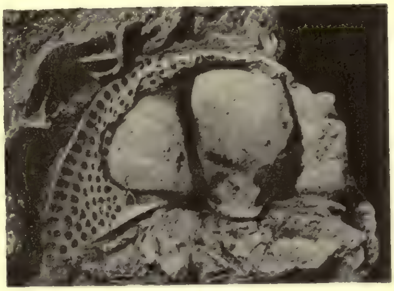
FIG. 12. Latex cast from external mould of same specimen. In. 49817*b*. ×2·5.

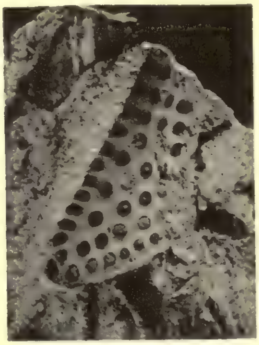

1

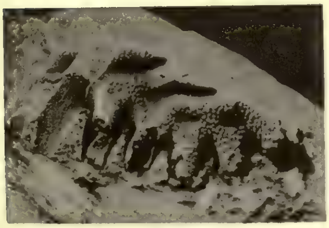

2

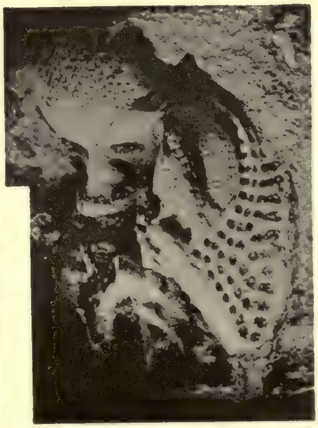

3

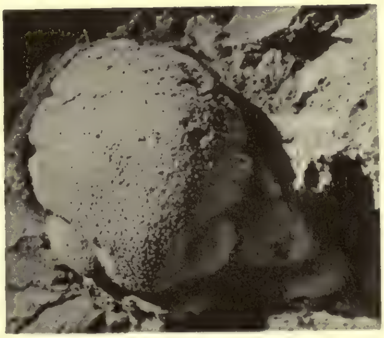

4

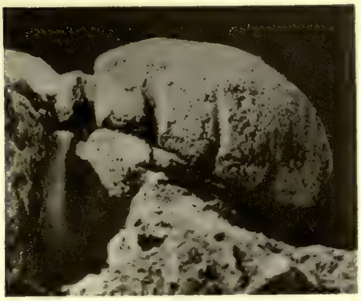

5

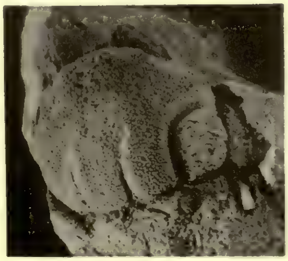

6

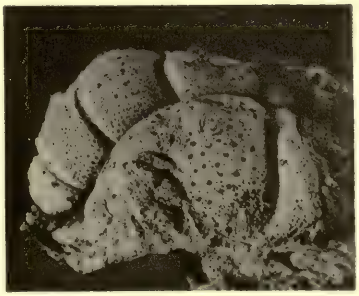

7


8


9


10


11


12

TRETASPIS, PSEUDOSPHAEREXOCHUS

PLATE 11

Encrinurus sp. . . . . p. 88

Upper Melmerby Beds, Upper Longvillian Substage, *Bancroftina robusta* Zone, Alston Road, locality H.

FIGS. 1, 4. Internal mould of pygidium. In. 49820. ×5.

Atractopyge scabra sp. nov. . . . . . . p. 91

Dufton Shales, Onnian Stage, *Onnia, superba* Zone, Pus Gill, locality A.5.

FIG. 2. Internal mould of cranidium. Holotype. In. 50154. ×3.

Dufton Shales, Pusgillian Stage, Swindale Beck, locality B. 25.

Fig. 3. Internal mould of cranidium, slightly compressed laterally. In. 50150. ×3.

Horizon as for Fig. 3, Pus Gill, locality A.25.

FIG. 10. External mould of pygidium. In. 50157*b*. ×4.

Atractopyge ? sp. . . . . p. 93

Corona Beds, Lower Longillian Substage, *Bancroftina type* Zone, Harthwaite Sike, locality E.3.

FIG. 5. Latex cast from external mould of fragmentary cranidium. In. 54638*b*. ×5.

Dindymene sp. . . . . p. 90

Dufton Shales, Upper Longvillian Substage, *Kjaerina typa* Zone, Swindale Beck, locality B. 5.

FIG. 6. Incomplete cranidium with test partially preserved. In. 49966. ×6.

Paracybeloides cf. *girvanensis* (Reed) . . . . p. 94

Horizon and locality as for Fig. 3.

FIG. 7. Internal mould of pygidium. In. 50177. ×3.

FIG. 9. Similar specimen showing development of spines near tip of pygidium. In. 50179. ×3.

FIG. 12. Latex cast from external mould of cranidium. In. 50158. ×2·25.

FIG. 14. Internal mould of incomplete librigena. In. 50172. ×2·5.

FIG. 15. Internal mould of cranidium. In. 50165. ×3.

Atractopyge ? sp. . . . . p. 93

Lower Melmerby Beds, Lower Longvillian Substage, Alston Road, locality J.

FIG. 8. Latex cast from exteral mould of cranidium. In. 54654*b*. ×4.

Paracybeloides sp. . . . . . . p. 95

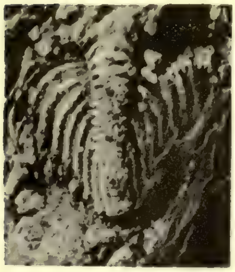
Horizon and locality as for Fig. 8.

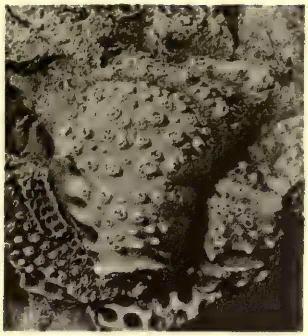
FIG. 11. Latex cast from external mould of pygidium. In. 54657. ×6.

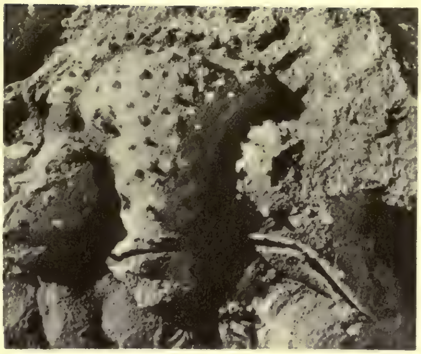
Dindymene duftonensis sp. nov. . . . . . p. 89

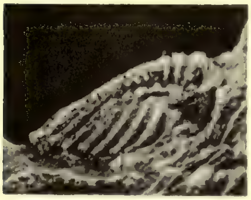
Dufton Shales, Marshbrookian Stage, probably topmost portion, Harthwaite Sike, locality E.12.

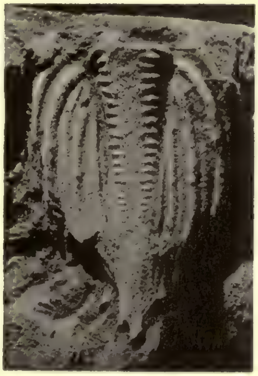
FIG. 13. Latex cast from external mould of incomplete cephalon. Holotype. In. 54652. ×6.

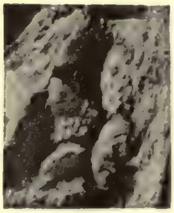

1

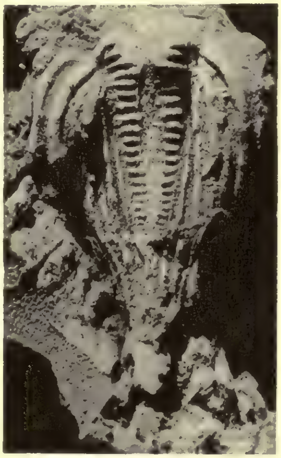

2

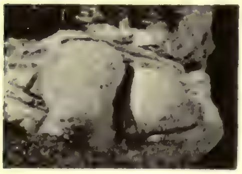

3

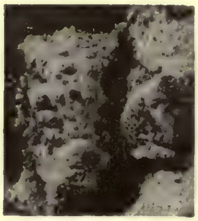

4

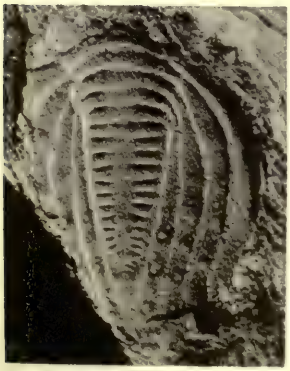

7

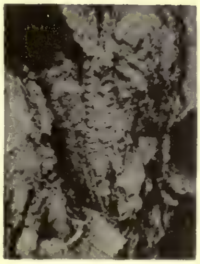

5

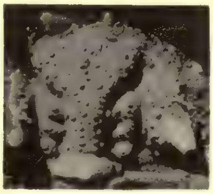

9

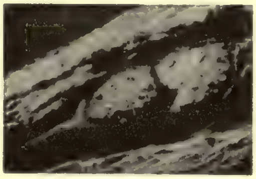

6

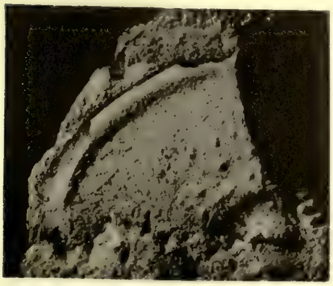

8

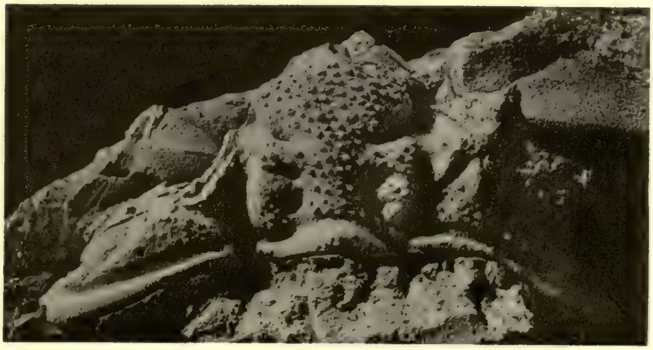

10


11


12


13


14


15

ATRACTOPYGE, DINDYMENE, ENCRINURUS, PARACYBELOIDES

PLATE 12

Dalmanitina mucronata matutina subsp. nov. . . . . p. 95

Dufton Shales, Pusgillian Stage, Pus Gill, locality A.7.

FIG. 1. Internal mould of incomplete cephalon. Paratype. In. 50112*a*. ×2·75.

Horizon as for Fig. 1, Swindale Beck, locality B.25.

FIG. 5. Internal mould of incomplete cranidium showing fixigenal spine. Paratype. In. 50113. ×2·75.

FIG. 6. Internal mould of pygidium. Holotype. In. 49905. ×2·75.

FIG. 9. Latex cast from external mould of fragmentary pygidium. Paratype. In. 49919. ×2·25.

FIG. 12. Internal mould of incomplete cranidium. Paratype. In. 50114*a*. ×2·25.

Estoniops alifrons (M'Coy) . . . . . p. 100

Caradoc Series, probably Upper Longvillian Substage, near Gelli Grin, Bala District.

FIG. 2. Internal mould of cephalon. GSM 19165. ×2·5.

Horizon as for Fig. 2, Capel Garmon, Denbighshire.

FIG. 4. Incomplete cephalon with part of test preserved. Lectotype, figured by M'Coy *in* Sedgwick & M'Coy, 1851, pl. 1.G, fig. 12. Sedgwick Museum A. 42694. ×1·5.

Dufton Shales, Upper Longvillian Substage, *Kjaerina typa* Zone, Swindale Beck, locality B. 7.

FIGS. 7, 13, 14. Cephalon with test preserved. In. 49837. ×3.

Horizon as for Fig. 7, Swindale Beck, locality B. 10.

FIGS. 8, 10. Pygidium with test preserved. In. 49839. ×2·5.

Duftonia lacunosa Dean . . . . . . p. 97

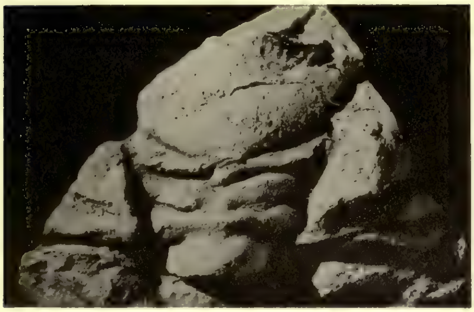
Horizon and locality as for Fig. 5.

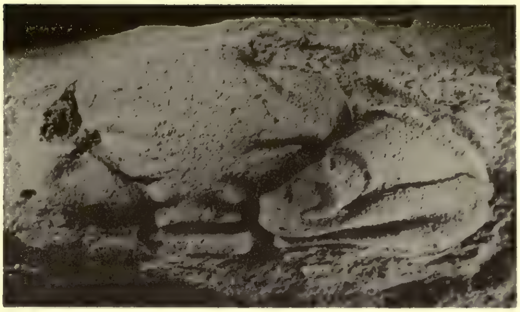
FIG. 3. Latex cast from external mould of cranidium. Holotype. In. 49824. ×3.

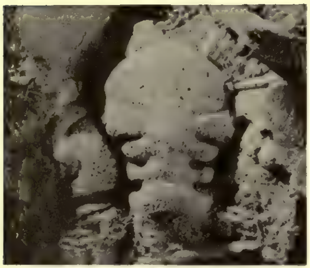
Kloucekia (*Phacopidina*) *apiculata* (M'Coy) . . . . p. 97

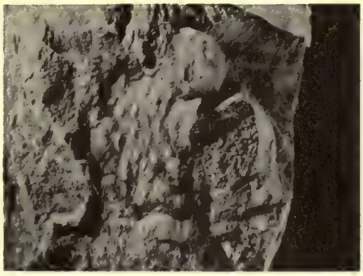
Upper Melmerby Beds, Upper Longvillian Substage, *Bancroftina robusta* Zone, Alston Road, locality H.

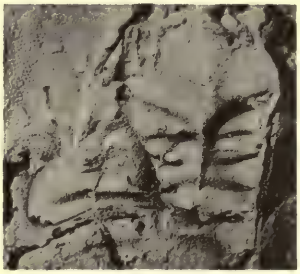
FIG. 11. Latex cast from external mould of fragmentary cranidium. In. 52587. ×3.

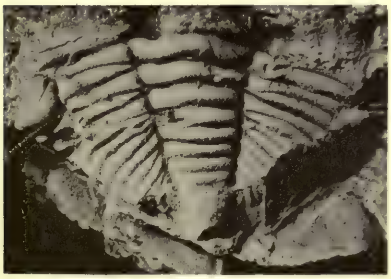

1

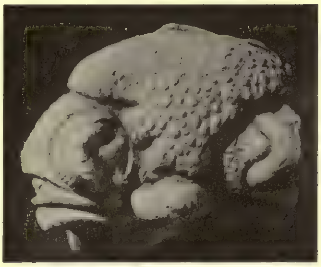

2

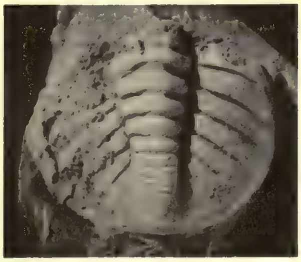

3


4

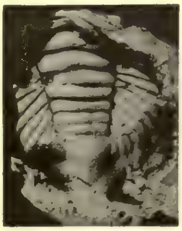

5

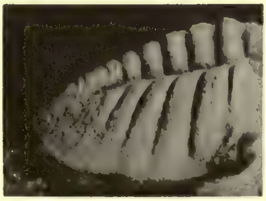

6

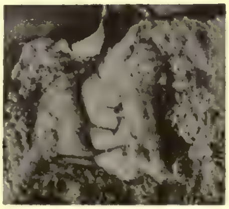

7

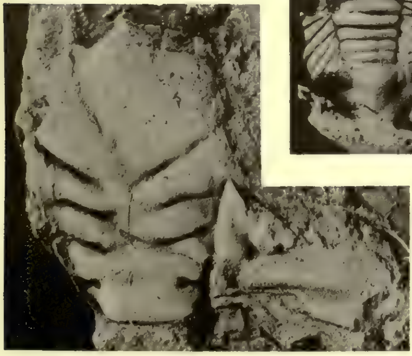

8

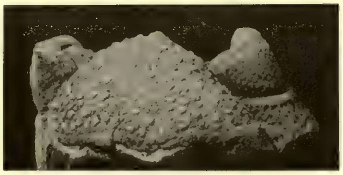
9

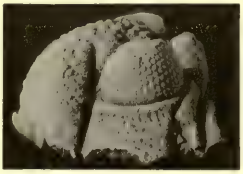



10


11


12


13


14

DALMANITINA, DUFTONIA, ESTONIOPS, KLOUCEKIA

PLATE 13

Calyptaulax planiformis sp. nov. . . . . . p. 98

Dufton Shales, Pusgillian Stage, Swindale Beck, locality B. 25.

FIG. 1. Latex cast from external mould of incomplete cranidium. Paratype. In. 49965*b*. ×2·75.

FIG. 2. Internal mould of distorted cranidium. Paratype. In. 49908. ×2.

FIG. 4. Internal mould of pygidium. Holotype. In. 50138. ×2.

FIG. 5. Internal mould of incomplete pygidium. Paratype. In. 49907. ×3.

Dufton Shales, Onnian Stage, *Onnia superba* Zone, Pus Gill, locality A.5.

FIG. 3. Internal mould of cranidium. Paratype. In. 49903. ×1·75.

Chasmops aff. *maxima* (Schmidt) . . . . p. 105

Horizon as for Fig. 1, Pus Gill, locality A. 28.

FIG. 6. Internal mould of fragmentary cranidium. In. 50412. ×3.

Onnicalymene onniensis (Shirley) . . . . p. 115

Horizon and locality as for Fig. 3.

FIG. 7. Cranidium with part of test preserved. In. 50294. ×3.

Chasmops cf. *extensa* (Boeck) . . . . p. 104

Dufton Shales, Actonian Stage, Swindale Beck, locality B. 15.

FIG. 8. Internal mould of pygidium. In. 49897*a*. ×2·75.

Gravicalymene jugifera sp. nov. . . . . . p. 116

Horizon as for Fig. 1, Swindale Beck, locality B. 30.

FIGS. 9, 11. Internal mould of almost complete individual, slightly compressed laterally. Paratype. In. 50245. ×1·5.

Flexicalymene cf. *caractaci* (Salter) . . . . p. 114

Lower Melmerby Beds, Lower Longvillian Substage, Alston Road, locality J.

FIG. 10. Internal mould of incomplete cranidium. In. 54658. ×2.

Chasmops sp. . . . . p. 105

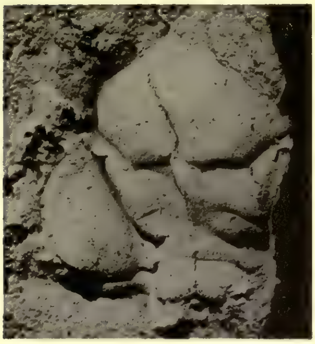
Horizon and locality as for Fig. 10.

FIG. 12. Latex cast of incomplete pygidium. In. 54656*b*. ×2.

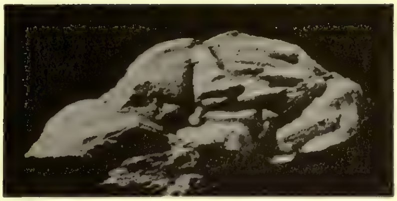
Diacalymene cf. *marginata* Shirley . . . . p. 116

Horizon and locality as for Fig. 1.

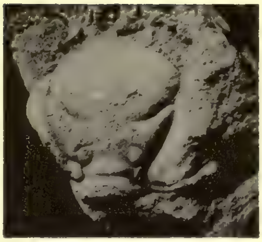
FIG. 13. Internal mould of incomplete cranidium, the frontal portion slightly compressed longitudinally. In. 50256. ×4·5.



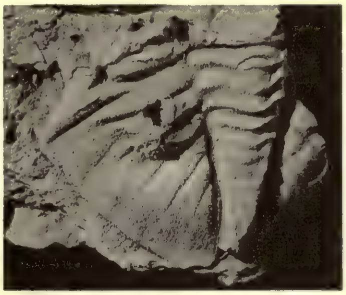
1



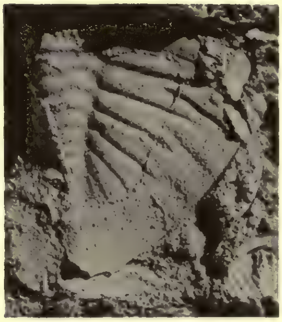
2



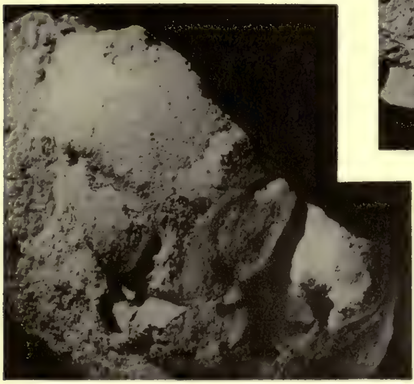
3



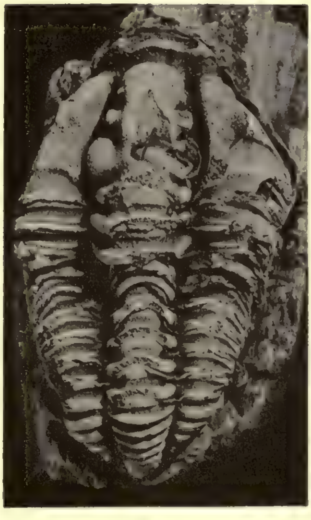
4



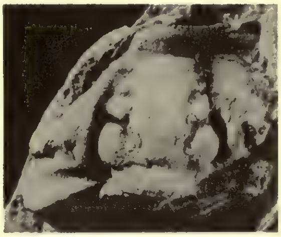
5



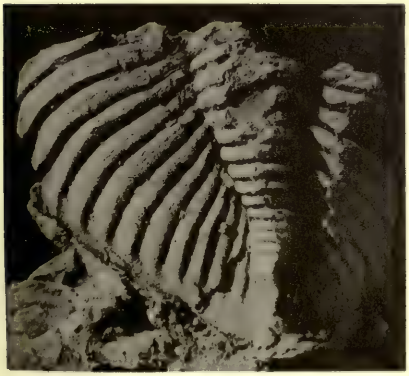
6



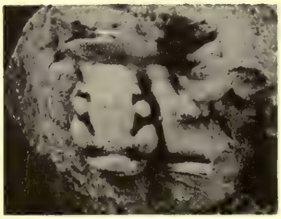
9



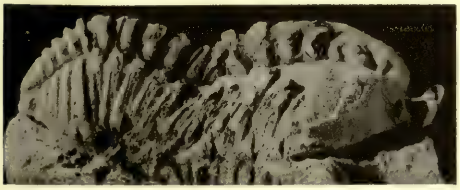
7



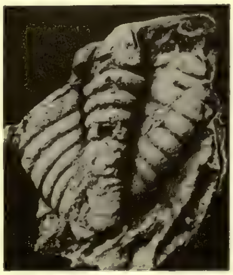
8



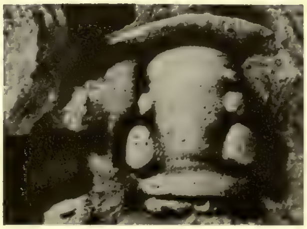
10



11



12



13

CALYPTAULAX, CHASMOPS, DIACALYMENE, FLEXICALYMENE, GRAVICALYMENE, ONNICALYMENE

PLATE 14

Onnicalymene onniensis (Shirley) . . . . . p. 115

Dufton Shales, Pusgillian Stage, Swindale Beck, locality B. 25.

FIG. 1. Internal mould of pygidium with attached thoracic segments. In. 50270. ×2·25.

FIGS. 2, 10. Internal mould of almost complete individual. In. 50266. ×1·75.

Horizon as for Fig. 1, Pus Gill, locality A. 28.

FIG. 7. Internal mould of large, incomplete cranidium. In. 50318*a*. ×2·75.

Gravicalymene jugifera sp. nov. . . . . . p. 116

Horizon as for Fig. 1, Swindale Beck, locality B. 28.

FIGS. 3, 4, 8. Almost complete cranidium with part of test intact. Holotype. In. 50263. ×1·75.

Horizon as for Fig. 1, Swindale Beck, locality B. 30.

FIG. 9. Internal mould showing pygidium and thorax. Paratype. In. 50245. ×1·5.

Onnicalymene laticeps (Bancroft) . . . . p. 115

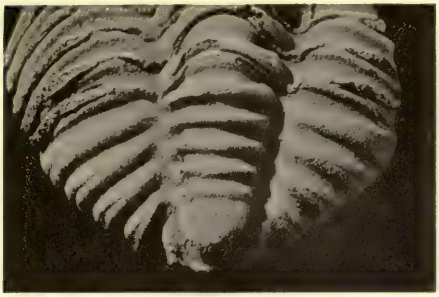
Dufton Shales, Actonian Stage, Swindale Beck, locality B. 15.

FIGS. 5, 6. Internal mould of cephalon with two attached thoracic segments. In. 50258. ×3.

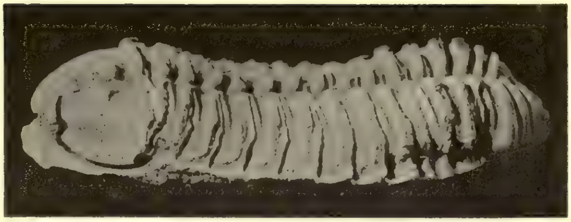
Diacalymene cf. *marginata* Shirley . . . . p. 116

Horizon and locality as for Fig. 1.

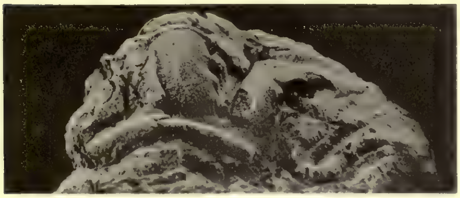
FIG. 11. Latex cast from external mould showing form of librigena, with conjugate fixigena and second glabellar lobe. In. 50254. ×1·75.



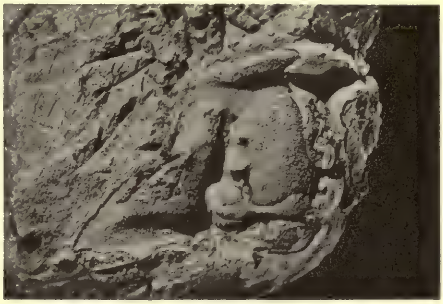
1



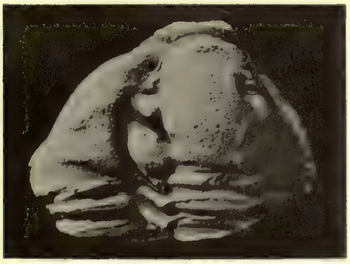
2



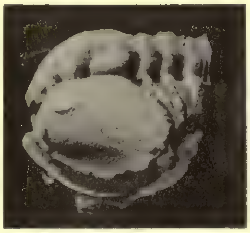
3



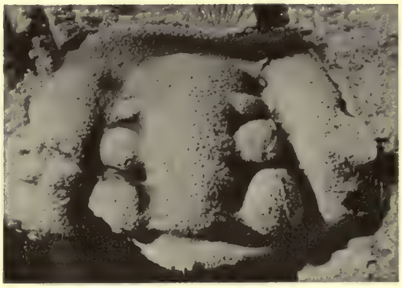
4



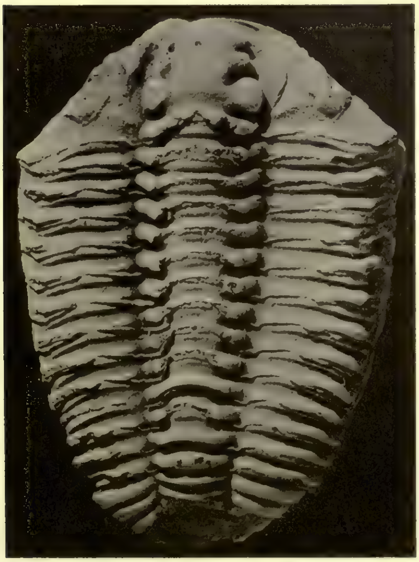
5



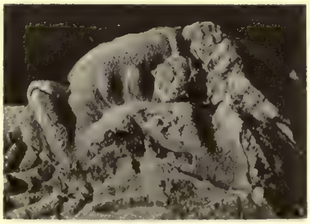
6



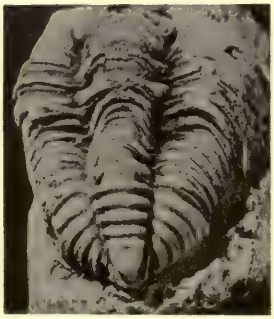
7



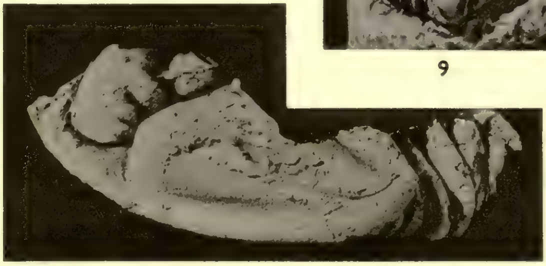
10



8



9



11

DIACALYMENE, GRAVICALYMENE, ONNICALYMENE

PLATE 15

Brongniartella ascripta (Reed) . . . . p. 106

Probably Lower Melmerby Beds, Lower Longvillian Substage, Alston Road, locality J.

FIG. 1. Incomplete, damaged cranidium. A. 29633. ×2.

FIG. 2. Internal mould of small cranidium. A. 29635. ×3. Figd. Reed, 1910, pl. 17, figs. 5, 7.

FIG. 5. Incomplete cranidium showing form of glabella. A. 29634. ×3. Figd. Reed, 1910, pl. 17, fig. 6.

FIG. 8. Internal mould of hypostoma. A. 29636*a*. ×6. Figd. Reed, 1910, pl. 17, fig. 8.

FIG. 11. Internal mould of incomplete cranidium showing median ridge. Holotype. A. 29632*a*. ×2·5. Figd. Reed, 1910, pl. 17, fig. 4.

Brongniartella minor (Salter) . . . . p. 106

Corona Beds, Lower Longvillian Substage, *Bancroftina typa* Zone, Pus Gill, locality A. 3.

FIG. 4. Internal mould of pygidium. In. 49844. ×2.

Brongniartella sp. . . . . . p. 108

Corona Beds, probably Lower Longvillian Substage, western flank of Roman Fell, exact locality unknown.

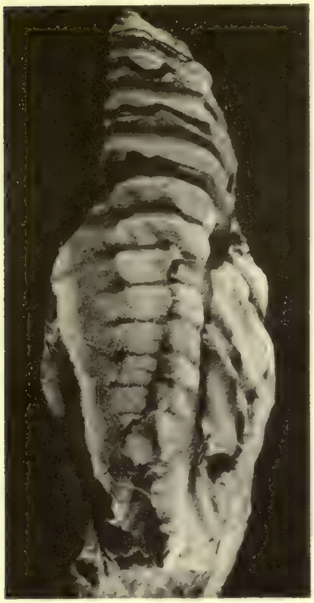
FIG. 3. Incomplete pygidium with part of thoracic axis. A. 32909. ×1·5.

FIG. 6. Slightly distorted cranidium. A. 32910. ×1·5.

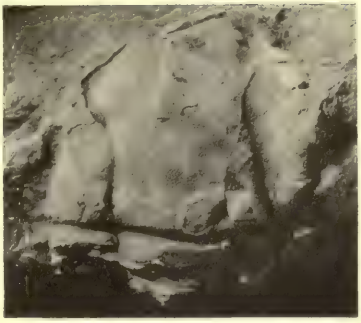
FIG. 7. Large pygidium with furrows exaggerated by crushing. A. 32911. ×1·4.

FIG. 9. Fragmentary pygidium with part of thorax. A. 32907. ×1·5.

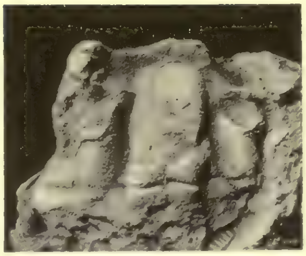
FIG. 10. Incomplete pygidium. A. 32908. ×1·8.



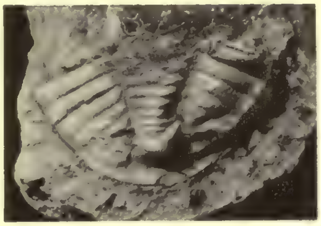
3



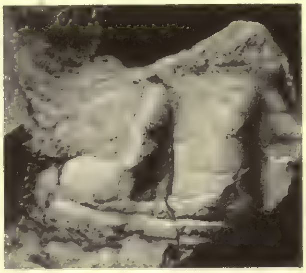
1



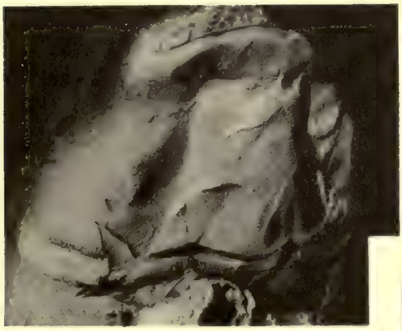
2



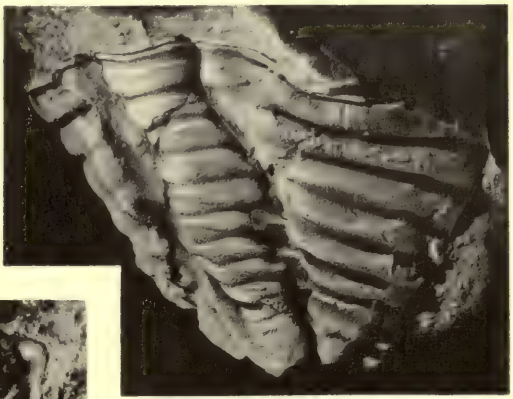
4



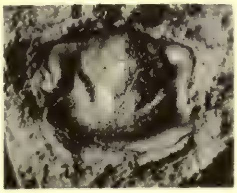
5



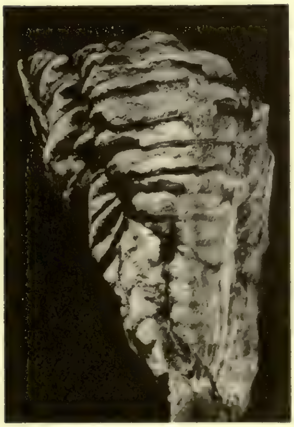
6



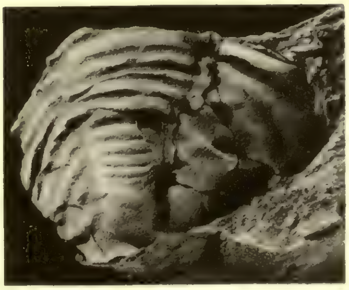
7



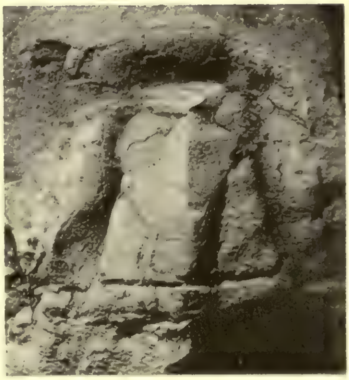
8



9



10



11

BRONGNIARTELLA

PLATE 16

Brongniartella depressa sp. nov. . . . . . p. 108

Dufton Shales, Pusgillian Stage, Swindale Beck, locality B. 25.

FIG. 1. External mould of cranidium. Holotype. In. 49882. ×2.

FIG. 7. Latex cast from external mould of incomplete thorax and pygidium. Paratype. In. 49881. ×2·5.

FIG. 10. External mould of almost complete pygidium. Paratype. In. 49884. ×2·5.

FIG. 13. Internal mould of immature cranidium showing traces of glabellar furrows. Paratype. In. 49885. ×2.

Toernquistia aff. *reedi* Thorslund . . . . p. 118

Lower Melmerby Beds, Lower Longvillian Substage, Alston Road, probably locality J.

FIGS. 2, 3. Internal mould of incomplete cranidium. A. 29960. ×8·5.

Proetidella ? *marri* sp. nov. . . . . . . p. 124

Corona Beds, Lower Longvillian Substage, zone of *Bancroftina typa*, Harthwaite Sike, locality E. 3.

FIG. 4. Internal mould of cranidium. Holotype. In. 54644. ×2·5.

FIG. 6. Internal mould of cranidium. Paratype. In. 54647. ×4.

FIG. 9. Latex cast of incomplete cranidium showing raised lines ornamenting surface of test. Paratype. In. 54646. ×2·5.

Brongniartella aff. *platynota* (Dalman) . . . . p. 110

Dufton Shales, Pusgillian Stage, Swindale Beck, locality B. 30.

FIG 5. Internal mould of incomplete pygidium. In. 49878. ×2·5.

Brongniartella bisulcata (M'Coy) . . . . . p. 108

Dufton Shales, Marshbrookian Stage, probably uppermost third, Swindale Beck, locality B. 14.

FIG. 8. Incomplete, slightly distorted cranidium. In. 49847. ×1·4.

Brongniartella minor (Salter) . . . . . p. 106

Horizon and locality as for Fig. 4.

FIG. 11. Internal mould of cranidium. In. 49840. ×2·2.

Stenopareia ? sp. . . . . p. 120

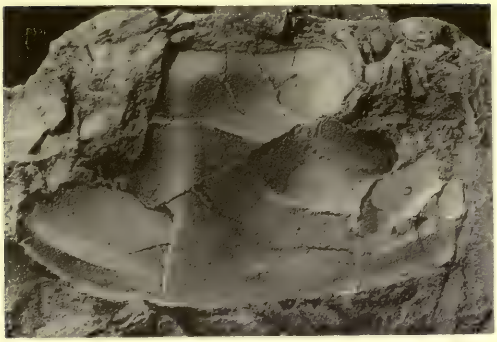
Horizon and locality as for Fig. 2.

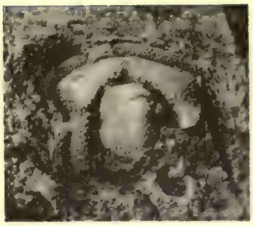
FIG. 12. Internal mould of pygidium. A. 29966. ×1·4.

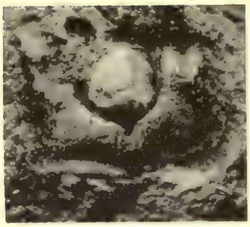
Brongniartella ascripta (Reed) ? . . . . . p. 107

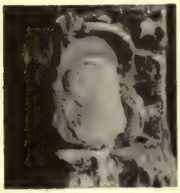
Horizon and locality as for Fig. 4.

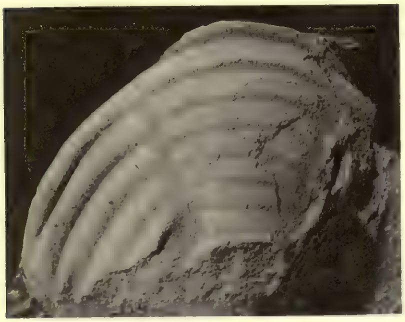
FIG. 14. Fragmentary internal mould of cranidium. In. 54639*a*. ×2·5.

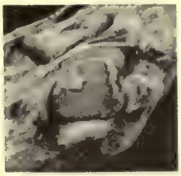

1

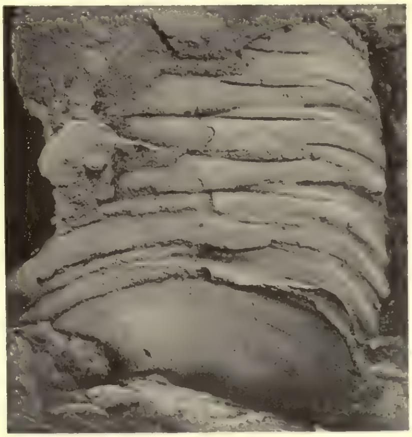

2

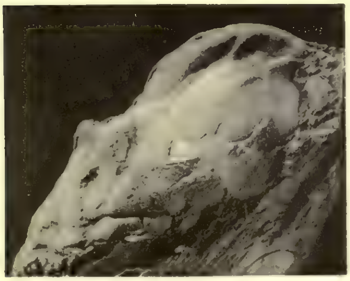

3

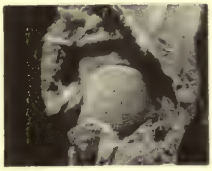

4

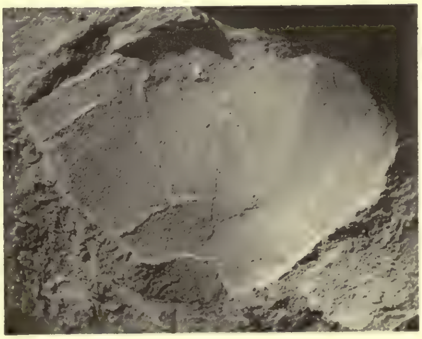

5

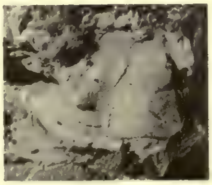

6

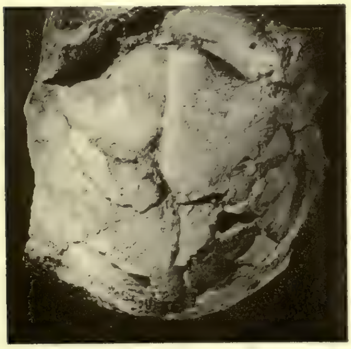

7

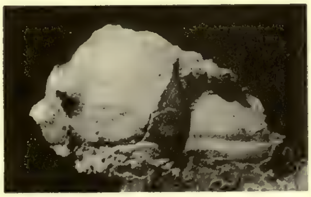

8

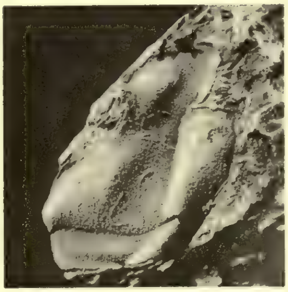

9


10


11


12


13


14

BRONGNIARTELLA, ILLAENUS, PROETIDELLA?, TOERNQUISTIA

PLATE 17

Platylichas cf. *laxatus* (M'Coy) . . . . . p. 121

Dufton Shales, Pusgillian Stage, Swindale Beck, locality B. 25.

FIG. 1. Internal mould of cranidium. In. 50115. ×2·5.

FIG. 7. Internal mould of pygidium. In. 50117. ×2.

Platylichas sp. . . . . p. 122

Upper Melmerby Beds, Upper Longvillian Substage, *Kjaerina bipartita* Zone, Alston Road, locality H.

FIG. 2. Internal mould of fragmentary pygidium. In. 52595. ×2·5.

Primaspis semievoluta (Reed) . . . . . p. 122

Lower Melmerby Beds, Lower Longvillian Substage, Alston Road, probably locality J.

FIGS. 3, 13. Internal mould of incomplete cranidium. Lectotype. A. 29951. ×3·5.

FIG. 10. Internal mould of small cranidium. Paratype. A. 29952. ×4.

FIG. 11. Internal mould of incomplete librigena. Paratype. A. 29954. ×3.

FIG. 15. Incomplete pygidium. Paratype. A. 29953. ×3·4.

Proetidella ? *marri* sp. nov. . . . . . . p. 124

Corona Beds, Lower Longvillian Substage, zone of *Bancroftina typa*, Harthwaite Sike, locality E. 3.

FIG. 5. Latex cast from external mould of cranidium. Paratype. In. 55882. ×2·5.

FIG. 6. Internal mould of pygidium. Paratype. In. 55882. ×3.

FIG. 8. Internal mould of cranidium. Holotype. In. 54644. ×2·5.

FIG. 9. Internal mould of librigena. Paratype. In. 54648. ×2·5.

Otarion sp. . . . . p. 123

Horizon and locality as for Fig. 2.

FIG. 4. Internal mould of cranidium. In. 49819*a*. ×12.

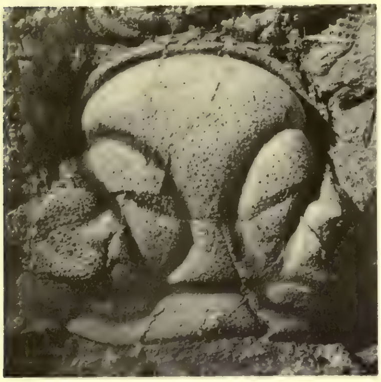
FIG. 12. Latex cast from external mould of same specimen. In. 49819*b*. ×12.

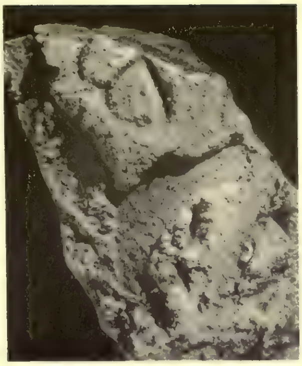
Conolichas melmerbiensis (Reed) . . . . . p. 120

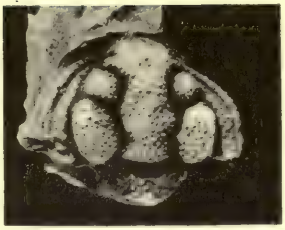
Horizon and locality as for Fig. 3.

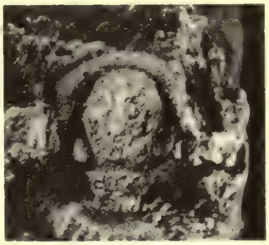
FIG. 14. Internal mould of hypostoma. Paratype. A. 29643. ×3.

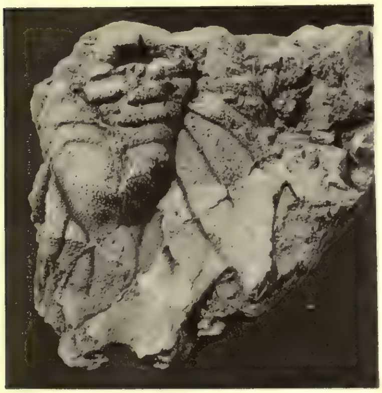
FIG. 16. Internal mould of incomplete cranidium. Paratype. A. 29641. ×1·6.

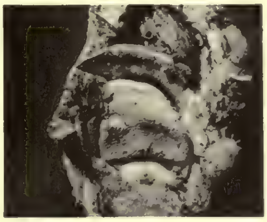

1

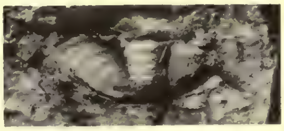

2

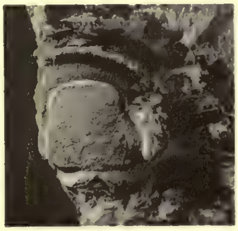

3

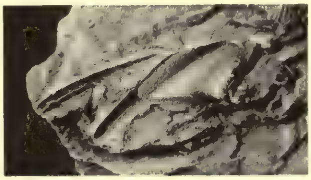

4

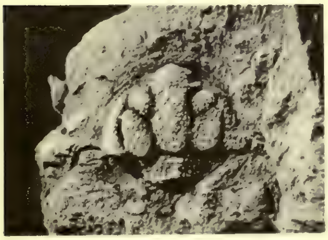

7

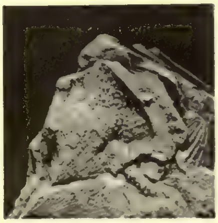

5

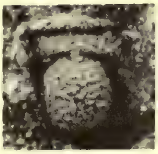

6

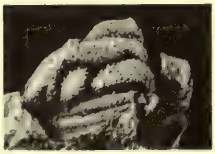

8

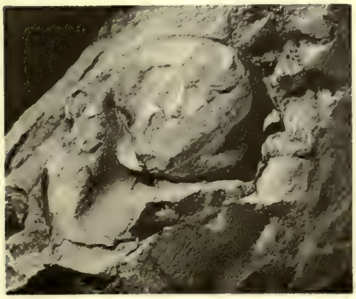

9

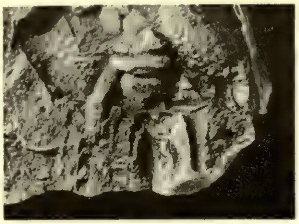

10

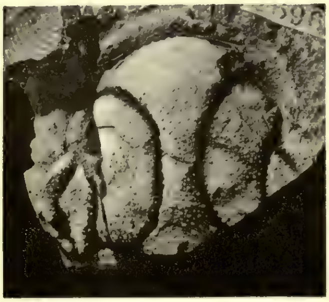

11


12


13


14


15


16

CONOLICHAS, OTARION, PLATYLICHAS, PRIMASPIS, PROETIDELLA?

PLATE 18

Conolichas melmerbiensis (Reed) . . . . . p. 120

Lower Melmerby Beds, Lower Longvillian Substage, Alston Road, probably locality J.

FIG. 1. Internal mould of almost complete individual. Paratype. A. 29637. ×1·7.

FIG. 2. Internal mould of pygidium. Paratype. A. 29642*a*. ×1·7.

FIGS. 3, 4. Internal mould of almost complete individual. Lectotype. A. 29638. ×1·7.

Remopleurides sp. . . . . . . p. 128

Dufton Shales, Onnian Stage, *Onnia gracilis* Zone, Pus Gill, locality A. 4.

FIG. 5. Internal mould of incomplete cranidium. In. 50129*a*. ×2·8.

Remopleurides sp. . . . . . . p. 127

Upper Melmerby Beds, Upper Longvillian Substage, *Kjaerina bipartita* Zone, Alston Road, locality H.

FIGS. 6, 10. Internal mould of distorted cranidium. In. 52594. ×2·4.

Remopleurides sp. . . . . . . p. 127

Dufton Shales, Actonian Stage, Swindale Beck, locality B. 15.

FIGS. 7, 8. Internal mould of cranidium. In. 50131. ×4·5.

Remopleurides sp. . . . . . . p. 128

Dufton Shales, Pusgillian Stage, Swindale Beck, locality B. 25.

FIG. 9. Underside of internal mould of left librigena. In. 50140. ×2·6.

FIG. 11. Internal mould of three conjoined thoracic segments. In. 50136*a*. ×3.

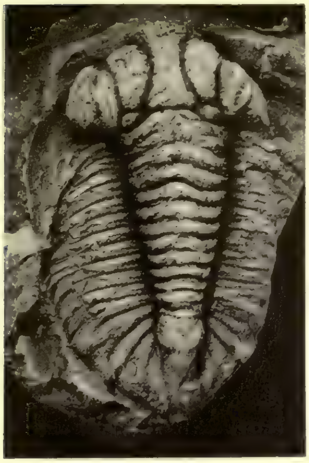
FIG. 13. Internal mould of flattened cranidium. In. 50135. ×2·2.

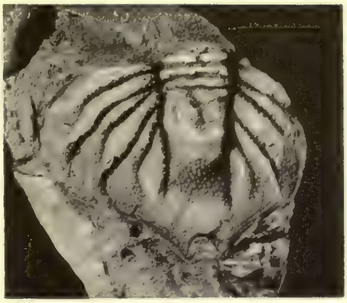
Remopleurides sp. . . . . . . p. 127

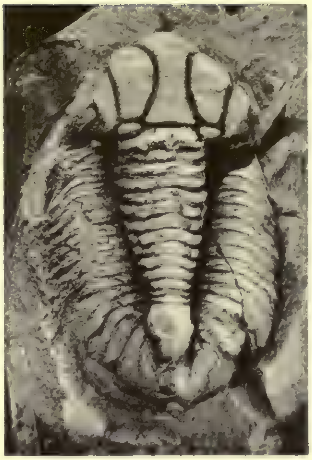
Lower Melmerby Beds, Lower Longvillian Substage, Alston Road, locality E.

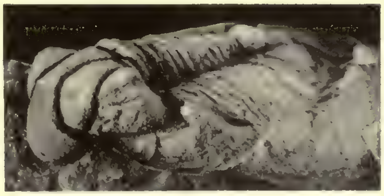
FIG. 12. Small, incomplete cranidium with most of test preserved. In. 52999. ×5.

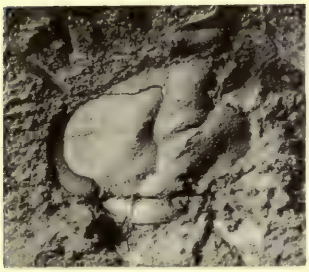
17 AUG 67

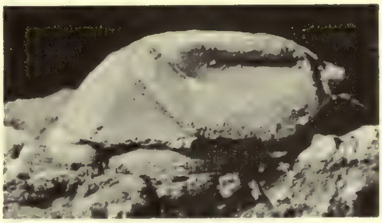

1

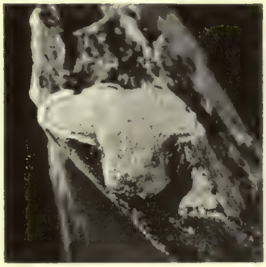

2

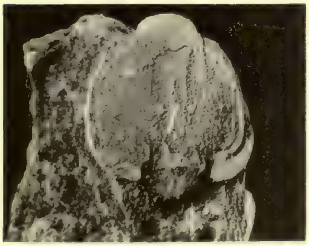

3

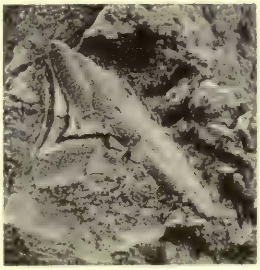

4

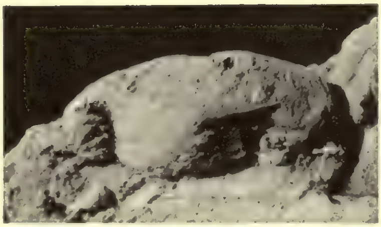

5

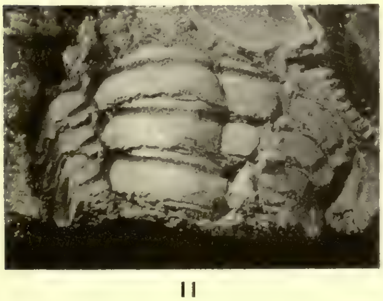

6

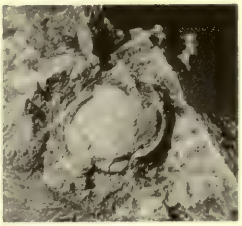

7

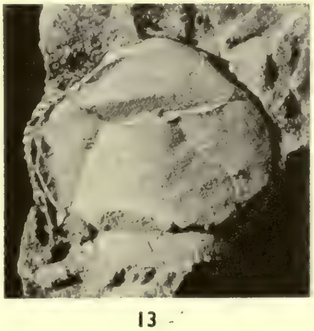

8


9


10


11


12


13

CONOLICHAS, REMOPLEURIDES

PRINTED IN GREAT BRITAIN BY
ADLARD AND SON, LIMITED
BARTHOLOMEW PRESS, DORKING

FOSSIL FLORA OF THE DRYBROOK SANDSTONE IN THE FOREST OF DEAN, GLOUCESTERSHIRE

K. M. LELE
AND
J. WALTON

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 7 No. 4
LONDON: 1962

FOSSIL FLORA OF THE DRYBROOK SANDSTONE IN THE FOREST OF DEAN, GLOUCESTERSHIRE

BY

K. M. LELE
(Birbal Sahni Institute, Lucknow)

AND

J. WALTON
(Professor of Botany in the University of Glasgow)

Pp. 135–152 ; *Plates* 19–23

2 2 AUG

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 7 No. 4
LONDON : 1962

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series, corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

This paper is Vol. 7, *No.* 4 *of the Geological (Palaeontological) series.*

© Trustees of the British Museum 1962

PRINTED BY ORDER OF THE TRUSTEES OF
THE BRITISH MUSEUM

Issued August 1962 *Price Twelve shillings and sixpence*

FOSSIL FLORA OF THE DRYBROOK SANDSTONE IN THE FOREST OF DEAN, GLOUCESTERSHIRE

By K. M. LELE & J. WALTON

SYNOPSIS

Descriptions of the fossil plants including *sporae dispersae* found in the Drybrook Sandstone (Mississippian) at Hazel Hill in the Forest of Dean, Gloucestershire are given. The most frequently occurring species are *Lepidophyllum fimbriatum* Kidston, *Scutellocladus variabilis* gen. et sp. nov. and *Diplopteridium holdeni* sp. nov. The spores belong to nineteen genera including three new species. A close comparison can be made between this flora and the flora of the Lower Brown Limestones at Diserth in North Wales and the age, judging from the plants, is that of the Calciferous Sandstone of Scotland. Palaeozoological evidence however supports a considerably later age.

INTRODUCTION

THE fossil plants described below were collected by Dr. H. S. Holden, Mr. F. M. Wonnacott, Mr. T. D. West, Mrs. C. J. Croucher and Mr. Keith Allen. Most of the specimens described are preserved in the British Museum (Nos. V.42428–43004, V.42048, V.42049), a few are in the Geological Museum, University of Birmingham (B.U. 800–804) while one is in the Hunterian Museum, University of Glasgow (No. Pb.3452). Preparations of the *sporae dispersae* isolated from the sandstone are now in the British Museum (Nos. V.43700–43734). In addition we have been kindly allowed to examine a collection made by members of the staff of the Geological Department, Kingston Technical College.

The specimens were all collected from a bed of fine sandstone with a grey to pink coloration in the Hazel Hill Quarry (Grid reference 32/646184) near Puddlebrook in Gloucestershire. The organic matter of the original plants is in the form of a black powder and only in exceptional cases (a few lepidophytes) is a cuticular membrane preserved. The forms of the plants are retained as a fine impression on the sandstone which is stained a brownish colour where it was in contact with the plant material. This helps to show up the shapes of the plants in photographs taken on orthochromatic plates.

The rock also contains somewhat poorly preserved spores. The *sporae dispersae* were isolated by macerating small fragments of the plant-bearing rock in cold concentrated hydrofluoric acid for about a week. The residue was washed free of the acid and the organic matter containing the microfossils was further separated by the swirling method (Funkhouser & Evitt, 1959 : 373). The material thus concentrated was directly mounted in glycerine jelly. Canada balsam and chloral hydrate were also found suitable for mounting. In favourable cases, grains were individually picked out and mounted for study. Staining with Safranin was found useful especially in case of lightly coloured spores. In view of the rather sparse spore population several macerations were made and nearly fifty slides were examined for the identification of spores. The number of better preserved and identifiable specimens is given in the description of each species. The system of classification used here is that of Potonié & Kremp (1955).

One of the most frequently occurring fossils, a lepidophyte sporophyll, *Lepidophyllum fimbriatum* Kidston has been described and figured by Allen (1961) and others under the name of *Lepidostrobophyllum fimbriatum* (Kidst.) but so far the generic name *Lepidostrobophyllum* has no valid basis and it is hoped that this nomenclatural confusion may be cleared up. The only animal fossil found associated with the plants is a Conulariid organism almost certainly of marine origin, which suggests that the sediments containing the plants were deposited near the sea in a lagoon or estuary.

In the earliest account of the geology of this area and on the one-inch, Old Series, sheets of the Geological Survey (43 S.E., 43 S.W. and 35) of the Forest of Dean, the Drybrook Sandstone is stated to be of Millstone Grit age. In the Geological Survey Memoir Trotter (1942 : 15, 16) divides the Drybrook Sandstone into upper and lower parts separated by the Drybrook Limestone or its equivalent. In the north the Coal Measures overlap, unconformably, the Lower Drybrook Sandstone. At Hazel Hill the sandstone rests on Limestones referred to zones C_2S_1 of the Avonian zone sequence and is overlain unconformably by the Coal Measures (Sibly & Reynolds, 1937 : 25, 37). Crookall (1939 : 72) assigns some obscure plant remains in the Drybrook Sandstone to ?*Cyclostigma*, a genus of Devonian plants, but they might well be the remains of a Carboniferous lycopod.

In the account that follows, descriptions are given of the most complete and identifiable specimens.

SYSTEMATIC DESCRIPTIONS

Genus ***SCUTELLOCLADUS*** nov.

DIAGNOSIS. Stems bearing narrow lanceolate, acuminate, falcate leaves. Leaves spirally arranged, almost contiguous, rhomboidal in section near their bases. On the smallest branches the leaves are more widely separated. On small branches which have lost their leaves the leaf scars are elliptical and level with the surface of the stem. A punctiform cicatrule is present in the centre of the scar. There are no persistent leaf bases or cushions and no evidence of a ligule or parichnos.

TYPE SPECIES. *Scutellocladus variabilis* sp. nov.

Scutellocladus variabilis sp. nov.

(Pl. 19, figs. 1–6)

DIAGNOSIS. As for the genus.

SYNTYPES. B.M.N.H. Nos. V.42433, V.42477, V.42538, V.42558.

LOCALITY. Hazel Hill Quarry, Puddlebrook, Forest of Dean, Gloucestershire.

HORIZON. Drybrook Sandstone. Mississippian.

DESCRIPTION. There is a number of examples of small branches of a plant with the appearance of a lycopod. Their stems vary in thickness from 1 mm. to 8 mm., some having their leaves still attached (Pl. 19, figs. 1, 2, 3, 5, 6) and some from which the leaves have fallen (Pl. 19, fig. 4). Where branching is seen it is dichotomous. The leaves vary from about 9 mm. to 5 mm. in length and from 2 mm. to 0·5 mm. in breadth. The leaves were acuminate, falcate and rhomboidal in section judging from the shape of their area of attachment to the stem (Pl. 19, fig. 1*a*). They were closely set on the stem in a spiral phyllotaxy. On one branch (Pl. 19, fig. 2), which is presumably at a later stage of development, the bases of the leaves which are still attached exhibit a narrow central vertical groove, are more widely spaced and are subcircular to elliptical in shape. The groove no doubt represents the vascular strand in the leaf base. On the smaller branches the leaves are attached by bases more elongated vertically and the scars are vertically elongated ellipses (1·8 × 1·5 mm.) with a central punctiform cicatrule (Pl. 19, fig. 4). The scar is flush with the surface of the branch and there is no elevated leaf base or cushion. This is evident when the profile of the branch is studied where it is seen to be almost straight. The scars measure about 1 mm. long by 0·7 mm. wide on the very smallest branches (Pl. 19, fig. 6).

There is no evidence of a ligule or parichnos on the leaves or on the defoliated branches. The complete absence of a persistent leaf cushion is a marked characteristic and the base of the leaf is not decurrent. There are some lycopod-like stems described by Radchenko (1956 : 199, pl. 36, figs. 1, 2 ; 1957 : 50, pl. 3, figs. 2, 3) under the name *Tomiodendron ostrogianum* (Zal.) which at first sight seem to resemble our fossils : but on closer examination it is clear that they had projecting persistent bases, in many cases decurrent, with a definite leaf-scar at the top of the cushion.

In addition to the compressions of small leafy branches assigned to *Scutellocladus variabilis* there are several examples (B.M.N.H., Nos. V.42459, V.42551, V.42557, V.42559) in which nothing but the cuticle remains in the form of a perforated lamina similar to the cuticles of *Bothrodendron tenerrimum* from the Moscow basin but lacking any trace of the cuticular linings of the ligular pits characteristic of that species. These Hazel Hill cuticles are from branches from about 8 mm. to over 13 mm. in diameter and may belong to *S. variabilis*.

Genus ***LEPIDOPHYLLUM*** Brongniart

Lepidophyllum cf. ***fimbriatum*** Kidston

(Pl. 20, figs. 18–20)

In addition to typical examples of *L. fimbriatum* (Allen, 1961 : 225) there is a number of lepidophyte leaves which are much longer, some reaching more than 6·5 cm. and about 6 mm. at the broadest part of the base (Pl. 20, fig. 20). The leaves taper very gradually to an acute apex. A single vein is visible in the middle and, while several have a smooth margin, two show rather widely spaced lateral hairs (Pl. 20, fig. 18) smaller than those of *L. fimbriatum* but of the same kind. If a sporangium had been present it must have been less than 6 mm. in width. A slight transverse cleft can be seen in one or two (Pl. 20, fig. 19) which might indicate the presence of a ligule. There is no film of carbonaceous matter at their proximal end as dense as that found on *L. fimbriatum* as described by Kidston (1883 : 543).

One can merely speculate as to the nature of these leaves. Perhaps they were the foliage leaves of the plant, either microsporophylls, sterile bracts of a strobilus, or intermediates between sporophylls and leaves.

There are some indubitable specimens of *L. fimbriatum* which measure only 8 mm. at the widest point and in the region where the sporangium was probably present are only 5 mm. wide.

Cf. ***Stigmaria***

(Pl. 19, fig. 7)

Two or three impressions of which the largest is shown in Pl. 19, fig. 7 are in the collection. They exhibit an extended smooth surface with one or more circular scars ranging from about 10 mm. to 12 mm. in diameter, each with a small central elevation. There scars closely resemble those on a *Stigmaria*. A large part of the surface shown uppermost in the figure has no such scars. In the Manchester Museum there is a similar specimen (Manch. Mus. CWM.23) which consists of a smooth surface, about 5 × 3 cm., on which there are two scars of the same kind. This specimen is from the Lower Brown Limestone at Diserth in North Wales. Another specimen from the same locality consists of a lepidophyte axis (Manch. Mus. LL.1190) 28 cm. long which tapers from 9·5 cm. in width at the base to 4 cm. at the top ; on which at the lower end there are similar large stigmarioid scars and on its upper two-thirds numerous regularly arranged small indentations or scars which are obviously the marks of leaf traces. As no leaf traces can be seen on the surface round the large scars it is unlikely that the large scars represent branch scars. These specimens are possibly parts of the base of a lepidophyte of comparable size to the " Naples tree " *Lepidosigillaria whitei* (Kräusel & Weyland, 1949 : 148) which has a slightly bulbous base with stigmarioid scars to which rooting appendages were attached.

Genus ***DIPLOPTERIDIUM*** Walton

Diplopteridium holdeni sp. nov.

(Pl. 20, figs. 8–15)

Diagnosis. Fronds tripinnatifid, from 10 cm. to 20 cm. long, ultimate divisions about 0·5 mm. in width. Main rachis from 2 mm. to 3·5 mm. broad at base ; forking equally into two main divisions. Pinnae borne on the two divisions of the frond and on the rachis below the fork. Some fronds have a naked rachis in the angle of the fork. Its first dichotomy is at right angles to the plane of the frond.

Holotype. B.M., V.42453.

Paratypes. B.M., V.42474, V.42487, V.43004.

Locality. Hazel Hill Quarry, Puddlebrook, Forest of Dean, Gloucestershire, England.

Horizon. Drybrook Sandstone ; Mississippian.

DESCRIPTION. The most noticeable and one of the most frequently occurring species found in the Hazel Hill quarry beds is a tripinnatifid frond which bears a close similarity to *Diplopteridium teilianum* (Kidston) which was found in beds assigned to the Upper Black Limestone near Prestatyn in North Wales. The fronds are, however, much smaller (Pl. 20, figs. 8–15) and the ultimate divisions of the pinnules narrower than those of *D. teilianum.* As far as one can judge from the fragments the fronds were probably from 10 cm. to 20 cm. in length and the main rachis, which in the specimens examined ranges from 2 mm. to 3·5 mm. in width, forked into two equal divisions in the middle of the frond. Near the proximal end of the frond (Pl. 20, fig. 9) the pinnae are small with few divisions and are opposite but higher up they increase in size and complexity and are alternate. They appear in many instances to have had their principal plane facing the rachis (Pl. 20, figs. 8, 10) so that as a result of compression the pinna at first sight resembles a *Rhacopteris* pinnule of the *R. petiolata* type and *Rhacopteris geikiei* Kidston (1923*a* : 218, text-fig. 11). The main rachis in one specimen (Pl. 20, fig. 9) appears to have been rugose. The arrangement of the pinnae in relation to the forking of the main rachis and their degree of subdivision is similar to that found in *D. teilianum.* Towards the ends of the two main divisions of the frond the pinnae become smaller and simpler and in the entire apex seen in Pl. 20, fig. 11 the rachis terminates in a single spatulate division.

Evidence for the presence of the fertile part of the frond, in the same position as that in specimens of *D. teilianum* (Walton, 1926 : 213, pl. 17, figs. 17–19), is afforded by one specimen (Pl. 20, fig. 8) where a bare rachis is seen as a continuation of the main rachis of the frond in the angle between the two divisions of the pinna-bearing parts of the frond. Careful examination reveals that the first forking of this presumably fertile rachis was a dichotomy at right angles to the plane of the frond. The presence of this structure in the angle of the fork supports the assignment of this plant to the genus *Diplopteridium.* Parts of the two divisions of a considerably larger frond (Pl. 20, fig. 13) have, situated between them, portions of a naked branching system (Pl. 13, fig. 13*x*) which probably represents the fertile part of the frond.

Genus ***SPHENOPTERIS*** Brongniart

Sphenopteris obfalcata Walton

(Pl. 20, figs. 16, 17)

Several fragmentary pieces of this frond from Hazel Hill (Pl. 20, figs. 16, 17) exhibit collectively features which justify identification with the type of this species from the Upper Black Limestones in N. Wales (Walton, 1931 : 363). The frond appears to have been at least tripinnatifid with a tendency for the pinnae to be opposite. The ultimate divisions and the form of the pinnae bear some resemblance to those of *Diplopteridium* but the ultimate divisions are more spatulate. There are several genera such as *Sphenopteris, Sphenopteridium, Spathulopteris* and *Rhodea* which have much divided fronds with fine ultimate segments and it is often difficult to decide to which genus such specimens as these should be assigned.

Sphenopteris cuneolata L. & H.

(Pl. 21, fig. 21)

Four incomplete specimens of a frond resembling *Sphenopteris cuneolata* L. & H. (Lindley & Hutton, 1837, pl. 214) occur in the collections from Hazel Hill. Kidston (1923 : 156) states that the type specimen is lost. The largest fragment (Pl. 21, fig. 21) probably represents part of a frond below the main fork, for the pinnae seem to get larger towards its distal end and are opposite. The rachis was evidently about 2 mm. thick as in Lindley & Hutton's figure. A smaller fragment (V.42048) with a rachis about 1·5 mm. thick has its pinnae alternately attached as in the upper divisions of the type. In the type and in the specimens from Hazel Hill several of the pinnae appear to be inaequilateral. This is due to folding of the pinnae as explained in the description of *Diplopteridium holdeni*. No venation is visible on the pinnules which have a finely striated surface. The base of the pinna is shortly decurrent on the rachis. The chief differences which exist between these specimens and the drawing of the type lie in the greater breadth of the frond and the wider spacing of the pinnules in the former. Kidston (1923 : 156) includes in the species a specimen of a frond from the Oil Shales, Calciferous Sandstone Series in Hailes Quarry near Edinburgh which differs very obviously from the type as figured by Lindley & Hutton (1837, pl. 214) in having definitely katadromic venation and in being irregularly and slightly lobed and unlike the type which, in common with the Hazel Hill specimens, has pinnately divided pinnae.

In view of the loss of the holotype the specimen described here (Pl. 21 fig. 21) is selected as the lectotype of *Sphenopteris cuneolata* L. & H.

Genus ***ARCHAEOPTERIDIUM*** Kidston

Archaeopteridium tschermaki (Stur)

(Pl. 21, fig. 22)

One specimen (B.U. 802) which we assign to this species (Pl. 21, fig. 22) consists of a clear impression on the fine sandstone of three pinnae attached to a piece of rachis. The shape and venation of the pinnules match exactly those of *Archaeopteridium tschermaki* (Stur) Kidston (1923 : 182) which has records in Britain ranging from the Limestone Coal Group down to the Oil Shale Group.

A second specimen (V.42498) which has smaller, more rounded pinnules or lobes with the same type of venation may also, perhaps, be assigned to this species.

FRUCTIFICATIONS

A considerable number of detached fructifications occur on the surfaces of the sandstone. Two types are of frequent occurrence and are in most cases on the same surfaces which have impressions of *Diplopteridium* fronds ; one must be referred to *Telangium* sp., the other seems to consist of bunches of cupules.

Telangium sp.

(Pl. 21, figs. 23–26)

There are several examples of fructifications consisting of a number of disc-like bodies connected in some instances by slender axes and each bearing numerous, pointed fusiform sporangia (Pl. 21, figs. 23–26). The individual sporangia appear to be about 1·3 mm long. There is a close resemblance in form and size between these fructifications and the *Telangium* found in connection with *Diplopteridium teilianum* (Kidston) (Walton, 1931, pl. 23, figs. 1, 3, 4). The sporangia of the *Telangium* found associated with *Sphenopteris affinis* L. & H. are from 2·5 mm. to 3·5 mm. in length while those associated with *Sphenopteris bifidum* are about 2 mm. long (Kidston, 1924 : 446, 454).

Calathiops sp.

(Pl. 21, figs. 27–29)

There are a number of examples of fructifications which consist of bunches of elongated structures which are considerably larger than the sporangia in the *Telangium* type. They probably were ovuliferous for in at least one example one of the bunches distinctly resembles an encupuled seed (Pl. 21, fig. 27*c*). Similar fructifications have been described by Kidston (1883 : 539, pl. 31, fig. 11) from the Cementstone Group in Liddesdale where they were found in masses in the shales. The name *Schützia* was later applied by Kidston (1924 : 424) to microsporangiate fructifications. We have decided, however, to include these fructifications of an indeterminate nature in the genus *Calathiops* of Goeppert.

Very probably these *Telangium* and *Calathiops* types represent pollen-bearing and ovuliferous organs of *Diplopteridium* as they are abundant on the same surface as the fronds of the latter.

SPORAE DISPERSAE

1. ***Leiotriletes sphaerotriangulus*** (Loose) Pot. & Kr.

(Pl. 21, figs. 30, 31)

Seven specimens ranging in size from 35 μ to 55 μ are closely similar to *Leiotriletes sphaerotriangulus* (Loose) Pot. & Kr. (1955 : 41). The trilete rays are distinct and almost reach the spore margin.

2. ***Punctatisporites minutus*** Kos.

(Pl. 21, figs. 32–34, ?35–37)

Small forms agreeing in size range with *P. minutus* Kosanke (1950 : 15) are not infrequent. The spore figured by Potonié & Kremp (1955, pl. 11, fig. 120) although smaller than the known size range (25–35 μ) seems indistinguishable from our specimens. The rays, in the present examples, are often eccentric and irregular. The exine usually shows an infrasculpture.

There are several other specimens (size range 18–40 μ) of a similar generalized pattern but having a thinner laevigate exine and thin or indistinct rays (Pl. 21, figs. 35–37). Although these specimens are provisonally placed under *P. minutus*, they might possibly belong to *Calamospora*.

Punctatisporites subobesus sp. nov.

(Pl. 21, figs. 38–42)

Diagnosis. Size range 45–80 μ (30 specimens); circular-subcircular; rays simple, more than ½ spore radius; exine commonly split open along the trilete mark to form a ± wide triangular fissure; folding along fissure occasional; exine up to nearly 4 μ thick, ± translucent, smooth to infrasculptured; folds uncommon.

Holotype. Pl. 21, fig. 40; 70 μ. B.M., V.43701.

Comparison. Spores similar to *P. obesus* (Loose) Potonié & Kremp (1955 : 43) in habit but distinguishable by their smaller size and longer trilete rays or fissure. Pl. 21, figs. 39–42 represent different degrees of the split trilete area. *P. fissus* Hoffmeister, Staplin & Malloy (1955 : 393) and *P. debilis* Hacquebard (1957 : 308) are distinguishable by their smaller size, thinner exine, shorter trilete area and granular sculpture.

4. ***Punctatisporites*** spp.

(Pl. 21, fig. 43)

The collection contains several specimens of *Punctatisporites* which cannot be specifically identified owing to their bad preservation or insufficient number. These spores range in size from 45 μ to 90 μ and may include more than one species. The spore in Pl. 21, fig. 43 has simple rays which reach the margin.

5. ***Calamospora*** sp. cf. ***C. mutabilis*** (Loose)

(Pl. 22, fig. 44)

Size range 82–115 × 30–43 μ (6 specimens), all folded into boat-shaped form; trilete mark seen only in one case (Pl. 22, fig. 44), rays thin, simple, longest ray 33 μ, a little more than ½ spore radius; exine moderately thin, smooth to faintly infrapunctate, yellow to brown in colour, with no difference in structure or colour in the contact area.

The spores, in most of their features, are comparable with *Calamospora mutabilis* (Loose) (see Potonié & Kremp, 1955 : 49 and Bhardwaj, 1957 : 82).

6. ***Granulatisporites tenuis*** sp. nov.

(Pl. 22, figs. 45, 46)

Diagnosis. Size range 17–25 μ (10 specimens), triangular to roundly triangular, rays distinct, occasionally with thin lips, reaching spore margin; exine crowded with very minute grana, about 20 grana between two rays on the margin; ornament present on rays.

HOLOTYPE. Pl. 22, fig. 45; 20 μ. B.M., V.43708.

REMARKS. The species is distinguished by its small size, minute grana and long rays bearing similar ornament.

7. ***Granulatisporites*** sp. cf. ***G. orbiculus*** (Pot. & Kr.)

(Pl. 22, figs. 47, 48)

Size range 24–35 μ (12 specimens), triangular to roundly triangular; rays extending almost up to spore margin; preservation of ornament poor, grana apparently somewhat irregular and partly coalescent. Nearest comparable species is *Granulatisporites* (*Cyclogranisporites*) *orbiculus* (Pot. & Kr) Potonié & Lele (1959).

8. ***Cyclogranisporites amplus*** McGregor

(Pl. 22, figs. 49–51)

Size range 50–90 μ (16 specimens); circular, trilete rays not always seen, $\frac{2}{3}$ spore radius or more; ornament of dense grana of variable size and shape, grana usually less than or up to 1 μ in diameter, over 100 grana at the margin, exine thickness variable, secondary folds common.

The present specimens fall within the size range of *C. amplus* McGregor and agree in most respects with it. It may be added that the ornament in *C. amplus* also appears to be rather variable as in the present forms (cf. McGregor, 1960, Pl. 11, fig. 8).

9. ***Cyclogranisporites*** sp.

(Pl. 22, fig. 52)

Size range 17–40 μ (20 specimens); circular, trilete mark weak, often not visible, when present rays $\frac{3}{4}$ spore radius or longer, ray ends often indistinct; exine thin, with frequent compression folds; ornamentation of densely set minute grana, grana ± variable in shape and size, often obscure on the equator; state of preservation unsatisfactory.

10. ***Planisporites minimus*** McGregor

(Pl. 22, figs. 53–55)

Size range 25–30 μ (4 specimens), triangular to nearly circular; rays indistinct, apparently long; ornament of minute coni or fine hairy spinules.

The few specimens in the present preparations do not represent the overall size range. They can, however, be assigned to *Planisporites minimus* McGregor (1960: 29, pl. 11, fig. 9) with which they agree most. It may also be remarked that the two species *P. minimus* McGregor and *P. delucidus* McGregor (1960: 30, pl. 11, fig. 16) are so similar in characters that they would appear to fall within the size range of a single species.

11. *Planisporites* sp. cf. *P. granifer* (Ibr.)

(Pl. 22, fig. 56)

Single specimen; 112 × 100 μ, triangular, corners rounded; triangular fold in the centre; exine with ± sparsely set short coni. The specimen is slightly larger but is comparable with *P. granifer* (Ibr.) Knox (cf. Potonié & Kremp, 1955 : 71; 1960 : 38).

12. *Verrucosisporites* sp.

(Pl. 22, fig. 57)

Specimens referable to *Verrucosisporites* are too few to justify specific determinations. Pl. 22, fig. 57 represents an example somewhat comparable with *V. donarii* Potonié & Kremp (1955 : 67).

13. *Camptotriletes* sp.

(Pl. 22, fig. 58)

Single specimen, 105 × 90 μ, roundly triangular, rays $\frac{2}{3}$ spore radius, ornament of verrucae up to 9 μ long and up to 8 μ broad, often connected to form crested ridges. The ornament of the exine supports the assignment of the specimen to *Camptotriletes*.

14. Cf. *Convolutispora* sp.

(Pl. 22, fig. 59)

A few specimens, showing somewhat convoluted ridges, are probably referable to *Convolutispora*. The specimen in Pl. 22, fig. 59 recalls *C. tessellata* H. S. & M. of Butterworth & Williams (1958, pl. 2, figs. 17, 18).

15. *Microreticulatisporites* cf. *cribellarius* (Horst)

(Pl. 22, figs. 60, 61)

Size range 40–55 μ (10 specimens), roundly triangular, rays distinct, extending up to the spore margin; reticulum imperfect, ± indistinct; lumina very small, muri low and barely evident at the margin.

The specimens are closely comparable with and probably indistinguishable from *Microreticulatisporites cribellarius* (Horst) Potonié & Kremp (1955 : 97).

16. *Microreticulatisporites* spp.

(Pl. 22, figs. 62, 63)

(i) Pl. 22, fig. 62:

Size range 65–78 μ (3 specimens); triangular to roundly triangular, thick rays almost reaching the equator, gnarled; muri 1–2 μ wide, not very high, lumina about equal to or slightly narrower than the width of muri; reticulum imperfect, apparently coarse, outline minutely undulating, about 20 curvatures between two rays at the margin, exine 2 μ thick.

(ii) Pl. 22, fig. 63 :

Size range 20–37 μ (a few specimens) ; triangular to ± circular ; rays indistinct, about ⅗ spore radius ; muri about 1 μ thick, close, irregular, anastomosing but no definite reticulum, margin minutely undulating, about 15–20 curvatures between two rays at the margin.

17. ***Dictyotriletes*** sp.

(Pl. 22, fig. 64)

Single specimen, probably comparable with *D. falsus* Potonié & Kremp (1955 : 109 ; Love, 1960, pl. 1, fig. 8).

Remarks. There are a few other ill-preserved specimens with somewhat projecting muri which are referable to *Reticulatisporites.* Besides these, one or two specimens may perhaps belong to *Knoxisporites.*

18. ***Lycospora*** cf. ***bracteola*** Butt. & Will.

(Pl. 22, fig. 65)

Size range 45–55 × 40–48 μ (6 specimens), width of cingulum of a spore often not uniform ; exine faintly granular, cingulum with much finer granules, visible only under high magnification.

The specimens are comparable with *L. bracteola* Butterworth & Williams (1958 : 357).

19. ***Lycospora*** spp.

(Pl. 22, figs. 66–69)

The genus is, on the whole, very poorly represented in numbers of spores, although more than one type is present. A few specimens with a narrow cingulum and a thickened inner zone (crassitudo) represents one type (Pl. 22, fig. 66). Another type (Pl. 22, fig. 67) somewhat recalls *L. granulata.* The form in Pl. 22, fig. 68 has a wider cingulum and a narrower inner crassitudo. The ornamentation of the cingulum varies from minute grana to short, narrow bacula. The specimen in Pl. 22, fig. 69 has a narrow membraneous cingulum, without a crassitudo. Types shown in Pl. 22, figs. 67–69 are solitary specimens.

20. ***Anulatisporites anulatus*** Pot. & Kr.

(Pl. 22, figs. 70, 71)

Size range 37–68 × 30–53 μ (12 specimens) ; usually oval, occasionally subtriangular ; cingulum ± ⅓ total spore radius, width often not uniform, outer margin smooth ; trilete mark indistinct to invisible, exine of central area and cingulum faintly infrasculptured.

The specimens bear close similarity to *A. anulatus* (Potonié & Kremp 1956 : 112). A few of them (Pl. 22, fig. 71), provisionally included under this species, have a comparatively narrower cingulum.

21. ?***Anulatisporites*** sp.

(Pl. 22, fig. 72)

Single specimen; 90 × 76 μ; oval; central area nearly triangular, thin; cingulum 25 μ wide, roughly equal to diameter of central area; a peripheral thickening (limbus?) about 2 μ wide evident; inner margin of cingulum also similarly thickened (about 2 μ); exine laevigate to infrasculptured; trilete mark not visible.

REMARKS. The essentially sculptureless cingulum, its smooth outline and apparent absence of a trilete mark favour the assignment of this specimen to *Anulatisporites*. However, a peripheral limbus-like thickening in *Anulatisporites* is hitherto unknown. The dark points seen on the cingulum in the photograph are due to foreign matter on the spore.

22. ***Densosporites*** sp.

(Pl. 23, fig. 73)

Single specimen; 56 × 48 μ; subcircular; central area infrapunctate; cingulum 13 μ wide, roughly equal to radius of central area, rugose in appearance owing to presence of irregular warts of variable size, specially towards the inner margin of cingulum where they appear to form a ± continuous, narrow, thickened ill-defined zone. The cingulum towards the periphery is finely wrinkled; outline nearly smooth; trilete mark invisible.

23. Cf. ***Cirratriradites*** sp.

(Pl. 23, fig. 74)

Single specimen; 70 × 48 μ; triangular; central body 40 × 30 μ, triangular, distinct; equitorial zone thin, about 12 μ wide, outline minutely crenulate; radial striations visible; trilete mark clear, rays extending beyond the central body; exine of central body and zone minutely granular-punctate.

The preservation of the spore is poor but its appearance supports an attribution to *Cirratriradites*.

24. ***Endosporites*** sp.

(Pl. 23, fig. 75)

Single specimen, 52·5 μ; subcircular; body 36 μ, circular, thin-walled; bladder nearly 10 μ wide, ± ½ radius of body, infrareticulate, with radial folds; outline smooth; trilete mark not seen.

25. ***Remysporites drybrookensis*** sp. nov.

(Pl. 23, figs. 76–81)

Cf. Radforth & McGregor, 1956 : 27, pl. 1, fig. 7.

DIAGNOSIS. Size range 70–155 × 70–128 μ (50 specimens); usually oval in outline, occasionally circular; central body large, 60–115 × 60–98 μ, distinct, often denser than the bladder, smooth, with frequent cracks, folds uncommon; bladder somewhat thick, apparently attached to the proximal side of body, smooth to faintly infrapunctate or infragranulate, folds uncommon; trilete mark often not evident, rays simple, often eccentric, ± half the length of the longer axis of the body.

HOLOTYPE. Pl. 23, fig. 76; 108 × 97 μ. B.M., V.43719.

REMARKS. The spores are referable to *Remysporites* Butt. & Will. *sensu* Potonié (1960: 72). They lack good proximo-distal orientation, with the result that the bladder may be more or less asymmetric and the trilete mark eccentric. The bladder width (compensated) ranges between 8–32 μ and is approximately $\frac{1}{4}$–$\frac{1}{12}$ of the longer axis of the body. The specimens, however, show all variations between the two extremes and may, therefore, be placed under the same species. The central body is variously cracked. There is often a concentric and ± continuous fissure along the margin of the body which produces a lighter zone between the body and the bladder (Pl. 23, figs. 76–80). In many cases, however, this fissure is absent (Pl. 23, fig. 81) and the crack is evidently not an original feature.

The present spores are distinguished from the known species of *Remysporites* (Butterworth & Williams, 1958; Staplin, 1960) by their consistently smooth and relatively thick body and bladder and the lack of secondary folds.

26. Cf. ***Remysporites*** sp.

(Pl. 23, fig. 82)

Two or three poorly preserved specimens. A more complete one (Pl. 23, fig. 82) measures 175 μ; body dense, 100 μ; bladder thin, as wide as the radius of body, folded over the central part; ornament obscure; trilete mark not seen. The spore recalls *Remysporites* in size and appearance but the bladder is somewhat broader (cf. Butterworth & Williams, 1958: 386).

27. SPORAE INSERTAE SEDIS

Pl. 23, fig. 83: Single specimen; 40 μ; triangular; central body convexly triangular, 25 μ; apparently enclosed by a rather thick structure (?capsula), outline of spore irregularly lobed; surface of spore laevigate but somewhat irregularly thickened at places to form small sinuous ridges (seen only by proper adjustment of focus). Spore pale yellow, transparent; trilete mark distinct, rays almost reaching equator of central body.

Pl. 23, fig. 84: Single specimen; 53 μ; roundly triangular; equitorial ridge (? cingulum) nearly 2·5 μ wide, about $\frac{1}{5}$ radius of central area; rays distinct, open, almost reaching margin of central area; exine of central area with irregular, large mounts; outline undulated.

THE AGE OF THE DRYBROOK SANDSTONE

There is a close lithological resemblance between the plant-bearing sandstones at Hazel Hill and the basement beds of the Lower Brown Limestone at Moel Hiraddug at Diserth, North Wales. In both, the sandstone is light coloured and friable and contains, associated with the plants, *Conularia* or Conulariid fragments, two from Hazel Hill (B.M., V.42431 and B.U. 800*a*) and numerous examples from Diserth (Manchester Museum, Cwm 3–28). There is also the occurrence in both places of specimens of smooth axes with stigmarioid scars which hitherto have not been observed elsewhere.

At the Diserth locality several examples of the fucoid *Chondrites plumosus* Kidston occur in association with abundant remains of *Lepidophyllum fimbriatum,* Kidston. These two fossils are also recorded by Kidston from the Cementstones at Glencartholm in the Borders. Among the specimens from Hazel Hill (e.g. B.M., V.42449) there are examples of a fucoid which consists of filaments 0·3 mm. in diameter and up to 9 cm. in length.

These facts suggest that the Hazel Hill and Diserth sediments were deposited in lagoons or estuaries near the sea and were of the same age as the lower part of the Calciferous Sandstone Series in the Borders.

The spores, on the whole, suggest a relatively simple and old type of assemblage in which *Punctatisporites* constitutes nearly half of the spore population and the *Azonotriletes* forms occur in far greater numbers than the *Zonales*. Very few examples of saccate genera except *Remysporites* are present. Monolete or monocolpate grains are apparently absent. Evidently, the Drybrook spore florule has little in common with the well-diversified and rich spore complex described by Butterworth & Williams (1958) from the Limestone Coal Group and the Upper Limestone Group of the Scottish Lower Carboniferous. The spore content of the Oil Shale Group (Love, 1960) which is comparable with that of Butterworth & Williams is also considerably varied and apparently younger than the Drybrook spore florule. Our present knowledge of the microspore assemblages from horizons older than the Oil Shales is very incomplete. It is, however, interesting to mention that Knox (1959 : 92) reports the occurrence of 13 genera from the base of the Calciferous Sandstone Series. They are *Punctatisporites, Calamospora, Granulatisporites, Cyclogranisporites, Lophotriletes, Apiculatisporis, Planisporites, Microreticulatisporites, Cristatisporites, Reticulatisporites, Lycospora, Densosporites* and *Cirratriradites*. Ten out of the above genera are also present in our assemblage. On the whole the Drybrook assemblage of sporae dispersae and that of the base of the Calciferous Sandstone Series show a close relationship with one another. We are inclined to believe that the Drybrook spore florule, like that of Knox, indicates a horizon fairly low in the Mississippian and supports the macrofossil evidence. On the other hand from the palaeozoological and stratigraphical evidence several geologists including Welch & Trotter (1960 : 60) place the Drybrook beds much higher and consider that they are in the Upper Caninia Zone C_2S_1. The North Wales floras from the Lower Brown and Upper Black Limestone like the Drybrook Sandstone flora are associated with marine animal fossils and may possibly have been developed under different ecological or climatic conditions from those prevailing in other areas during the Lower Carboniferous and this might account for the difference in the floristic composition between them and floras of the same age in other parts.

ACKNOWLEDGEMENTS

We cordially thank those mentioned in the Introduction, Dr. Isles Strachan of the University of Birmingham, who kindly lent its collection to us, and the staff of the Geological Department of Kingston Technical College for lending specimens which they had collected. To the Staff of the Department of Palaeontology, Natural History Museum, London, we are especially grateful for their help and encouragement and we thank Mr. W. Anderson for assisting us with the photography.

One of us (K. M. L.) thanks the authorities of the Colombo Plan for the award of a scholarship, and the Director, Birbal Sahni Institute of Palaeobotany, Lucknow, India, for the grant of study leave.

REFERENCES

Allen, K. C. 1961. *Lepidostrobophyllum fimbriatum* (Kidston, 1883) from the Drybrook Sandstone (Lower Carboniferous). *Geol. Mag. Lond.*, **98** : 225–229, pl. 13.

Bhardwaj, D. C. 1957. The palynological investigations of the Saar Coals, Pt. 1. Morphology of sporae dispersae. *Palaeontographica*, Stuttgart, **101**, B : 73–125, pls. 22–31.

Butterworth, M. A. & Williams, R. W. 1958. The small spore floras of coals in the Limestone Coal Group and Upper Limestone Coal Group and Upper Limestone Group of the Lower Carboniferous of Scotland. *Trans. Roy. Soc. Edinb.*, **68** : 353–390, pls. 1–4.

Crookall, R. 1939. Lycopodiaceous stems (? *Cyclostigma Kiltorkense* Haughton) from Mitcheldean in the Forest of Dean. *Bull. Geol. Surv. Gt. Britain*, London, **2** : 72–77, pls. 5, 6.

Funkhouser, J. W. & Evitt, W. R. 1959. Preparation techniques for acid-insoluble microfossils. *Micropaleont.*, New York, **5** : 369–375, 2 figs.

Hacquebard, P. A. 1957. Plant spores in coal from the Horton Group (Mississippian) of Nova Scotia. *Micropaleont.*, New York, **3** : 301–324, pls. 1–3.

Hoffmeister, W. S., Staplin, F. L. & Malloy, R. E. 1955. Mississippian plant spores from the Hardinsburg formation of Illinois and Kentucky. *J. Paleont.*, Chicago, **29** : 372–399, pls. 36–39.

Kidston, R. 1883. Report on fossil plants collected by the Geological Survey of Scotland in Eskdale and Liddesdale. *Trans. Roy. Soc. Edinb.*, **30** : 531–550, pls. 30–32.

—— 1923. Fossil plants of the Carboniferous rocks of Great Britain. *Mem. Geol. Surv. Gt. Brit., Palaeont.*, **2**, 2 : 111–198, pls. 23–47.

—— 1923*a*. Fossil plants of the Carboniferous rocks of Great Britain. *Mem. Geol. Surv. Gt. Brit. Palaeont.*, **2**, 3 : 199–274, pls. 48–68.

—— 1924. Fossil plants of the Carboniferous rocks of Great Britain. *Mem. Geol. Surv. Gt. Brit. Palaeont.*, **2**, 5 : 377–522, pls. 92–122.

Knox, E. M. 1959. Some aspects of microspore morphology. *Trans. Bot. Soc. Edinb.*, **38** : 89–99, 27 figs.

Kosanke, R. M. 1950. Pennsylvanian spores of Illinois and their use in correlation. *State Geol. Surv. Illinois*, **74** : 1–128, pls. 1–16.

Kräusel, R. & Weyland, H. 1949. *Gilboaphyton* und die Protolepidophytales. *Senckenbergiana*, Frankfurt a.M., **30** : 129–152, pls. 1–7.

Lindley, J. & Hutton, W. 1837. *The Fossil Flora of Great Britain*, **3**, pls. 157–230. London.

Love, L. G. 1960. Assemblages of small spores from the Lower Oil Shale Group of Scotland. *Proc. Roy. Soc. Edinb.*, **67** : 99–126, pls. 1, 2.

McGregor, D. C. 1960. Devonian spores from Melville Island, Canadian Arctic Archipelago. *Palaeontology*, London, **3** : 26–44, pls. 11–13.

Potonié, R. 1960. Synopsis der Gattungen der sporae dispersae. *Beih. Geol. Jb.*, Hanover. **39**, 3 : 1–189, pls. 1–9.

POTONIÉ, R. & KREMP, G. O. W. 1955. Die sporae dispersae des Ruhrcarbons. *Palaeontographica*, Stuttgart, **98**, B : 1–136, pls. 1–16.

—— —— 1956. Die sporae dispersae des Ruhrcarbons. *Palaeontographica*, Stuttgart, **99**, B : 85–191.

POTONIÉ, R. & LELE, K. M. 1959. Studies in the Talchir flora of India—Sporae dispersae from the Talchir Beds of South Rewa Gondwana Basin. *Palaeobotanist*, Lucknow, **8** : 22–37, pls. 1–3.

RADCHENKO, G. P. 1956. New families and genera of fossil plants, II. *All Union Inst. Geol. Res.* (n.s., Palaeont.), **12** : 185–264. (In Russian.)

—— 1957. Morphological and anatomical peculiarities of some early Carboniferous vegetative types from Kouznetsk Province. *Kryshtofovich Memorial Volume*, pp. 33–54, pls. 1–4. Moscow & Leningrad.

RADFORTH, N. W. & MCGREGOR, C. 1956. Antiquity of form in Canadian plant microfossils. *Trans. Roy. Soc. Canada*, Ottawa (3, 5) **50** : 27–33, pls. 1–3.

SIBLY, T. F. & REYNOLDS, S. W. 1937. The Carboniferous Limestone of the Mitcheldean area, Gloucestershire. *Quart. J. Geol. Soc. Lond.*, **93** : 23–51.

STAPLIN, F. L. 1960. Upper Mississippian plant spores from the Golata Formation, Alberta, Canada. *Palaeontographica*, Stuttgart, **107**, B : 1–40, pls. 1–8.

TROTTER, F. M. 1942. Geology of the Forest of Dean Coal and Iron Ore Field. *Mem. Geol. Surv.Gt. Britain*, London. vi + 95 pp., 5 plates.

WALTON, J. 1926. Contributions to the knowledge of Lower Carboniferous plants, Pts. I, II. *Philos. Trans.*, London (B) **215** : 201–224, pls. 16, 17.

—— 1931. Contributions to the knowledge of Lower Carboniferous plants, Pt. III. *Philos. Trans.*, London (B) **219** : 347–379, pls. 23–26.

WELCH, F. B. A. & TROTTER, F. M. 1960. Geology of the Country around Monmouth and Chepstow. *Mem. Geol. Surv. Gt. Britain*, London. viii + 164 pp., 2 pls.

PLATE 19

Scutellocladus variabilis gen. et. sp. nov.

FIG. 1. Leafy branch with closely set leaf-bases. B.M., V.42433. Nat. size. Syntype.

Fig. 1*a*. Part of the same specimen. × 3.

FIG. 2. Small forking branch with leaves still attached showing the areas of attachment of the leaves with a longitudinal ridge representing the leaf trace. B.M., V.42538. × 3. Syntype.

FIG. 3. Dichotomously forking leafy branch. B.U. 800. Nat. size.

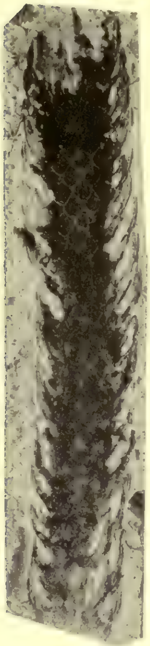
FIG. 4. Dichotomously forking branch showing leaf-scars with central punctiform scar. B.M., V.42558. × 4.

FIG. 5. Small leafy twig. The apical region of one branch is seen. B.M., V.42477. Nat. size.

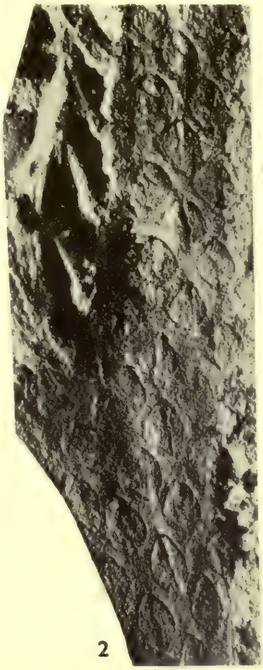
FIG. 6. Smallest size of leafy branch found. U.G. Pb.3452. Nat. size.

Cf. *Stigmaria*

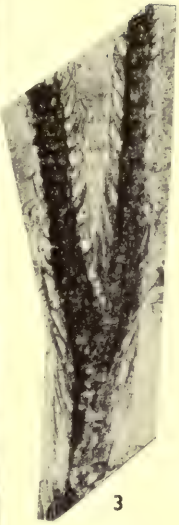
FIG. 7. Impression of the outer surface of an axis bearing a number of stigmarioid scars. B.M., V.42428. Nat. size.



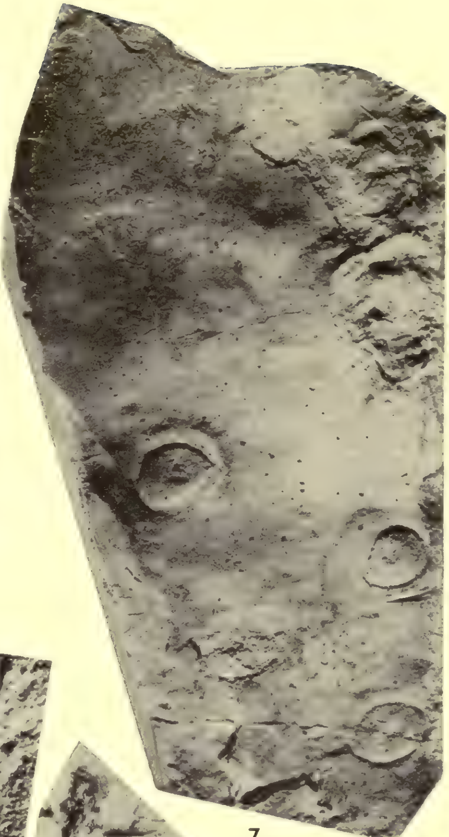
1



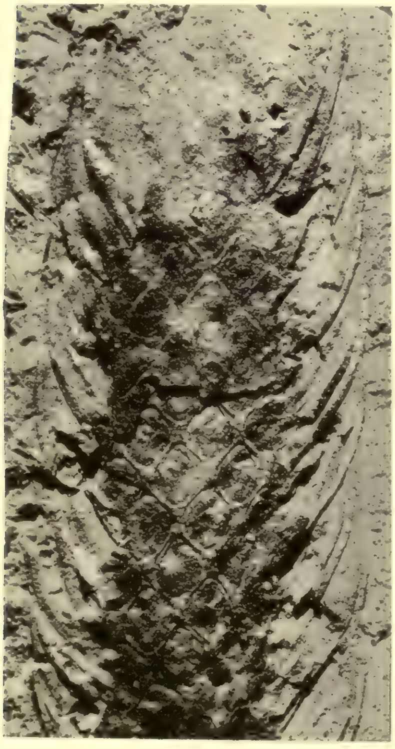
2



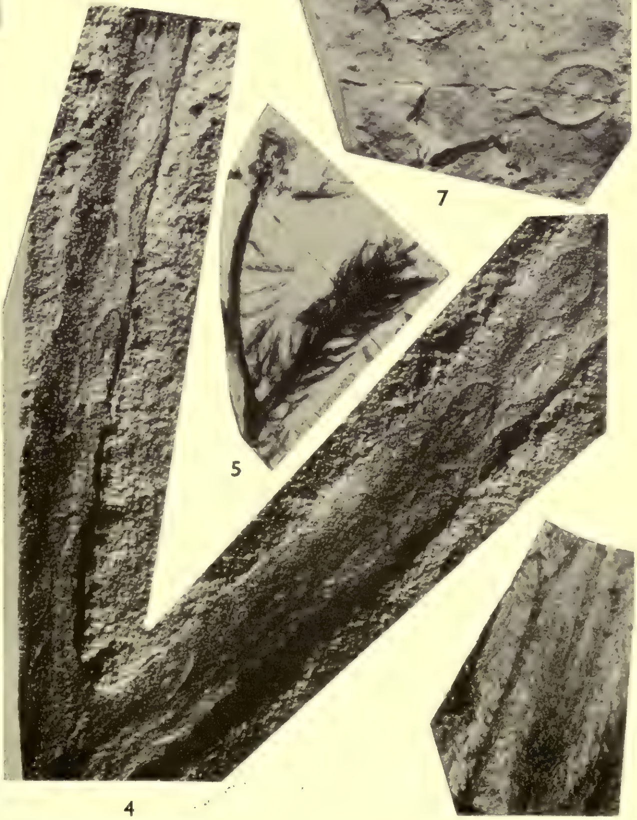
3



7



1a



4

5

6

LELE & WALTON

PLATE 20

All figures are natural size

Diplopteridium holdeni sp. nov.

Fig. 8. Specimen showing central part of a frond with remains of fertile rachis. B.M., V.42453. Holotype.

Fig. 9. Base of a frond with small basal pinnae. B.M., V.43004. Paratype.

Fig. 10. Part of a frond showing apparently inaequilateral pinnules on the pinnae. B.M., V.42487. Paratype.

Fig. 11. The two terminal portions of a frond. B.U. 804*a*.

Fig. 12. Parts of the two divisions of a frond showing clearly the form of the pinnae. B.M., V.42524.

Fig. 13. Part of the largest frond. Portions of its two divisions on the left and right and parts of presumably its fertile rachis (*x*) between. B.U. 804.

Fig. 14. Middle part of an apparently sterile frond. B.M., V.42474. Paratype.

Fig. 15. Parts of a frond with very slender ultimate segments. B.M., V.42457.

Sphenopteris obfalcata (Walton) n. comb.

Fig. 16. ?Main rachis of a frond with proximal parts of six subopposite primary pinnae· B,U. 803.

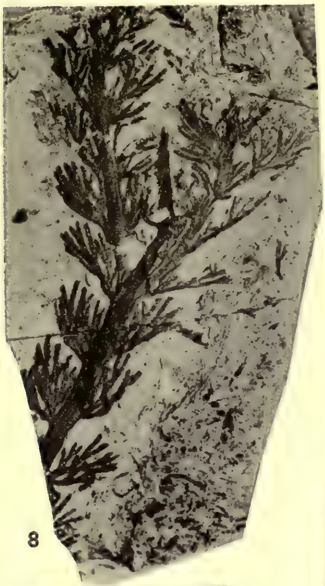
Fig. 17. Part of a frond to show form of pinnae and their ultimate divisions. B.M., V.42488.

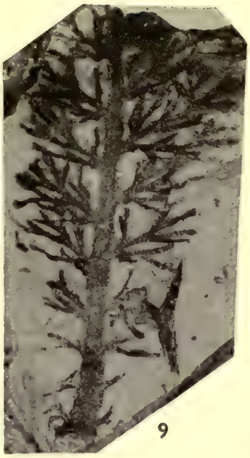
Lepidophyllum cf. *fimbriatum* Kidston

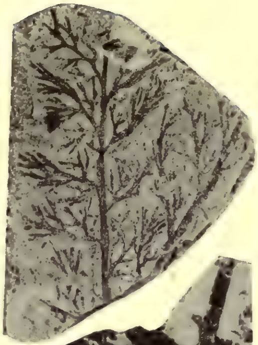
Fig. 18. Distal part of a leaf with a single row of short hairs on each side. B.M., V.42516.

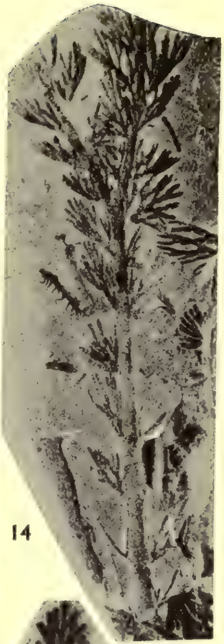
Fig. 19. Almost complete leaf showing expanded base. No hairs are evident. B.M., V.43442.

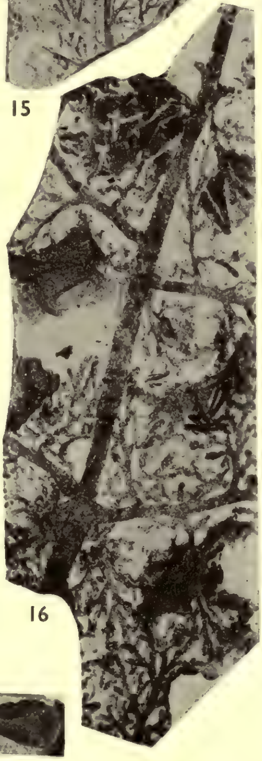
Fig. 20. Complete leaf showing acute apex. B.M., V.42531.

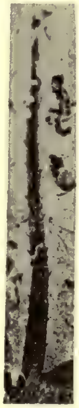

8


9

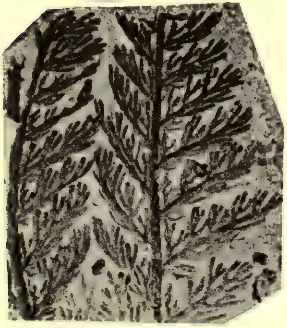

15

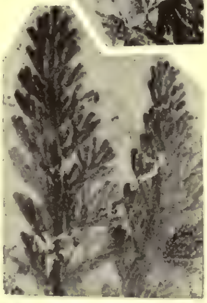

14

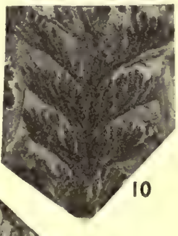

16

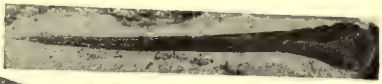

18

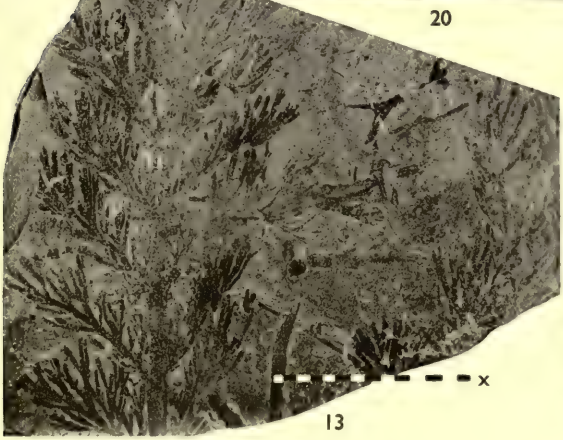
19


12

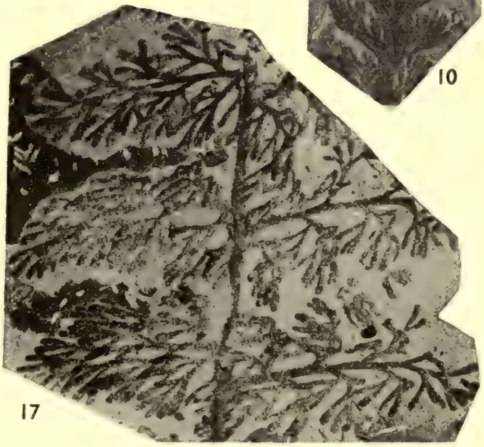

11


10


20



13


17

LELE & WALTON

PLATE 21

Sphenopteris cuneolata L. & H.

FIG. 21. Part of a frond with parts of nine pairs of pinnae. Lectotype ; B.U.801. Nat. size.

Archaeopteridium tschermaki (Stur) Kidston

FIG. 22. Parts of three pinnae. B.U.802. ×2.

Telangium sp.

FIGS. 23, 24, 25 and 26. Groups of fructifications which appear to consist of microsporangia attached to discs at the ends of slender rachides. 23, 24 B.U.802 and B.U.800 ; 25, 26 B.M., V.42435 and V.43443. ×3.

Calathiops sp.

FIG. 27. Fructification with a cupule *c*, probably ovuliferous, shown at *c*. B.M., V.42432. ×3.

FIG. 28. Fructification probably ovuliferous. B.U.802*a*. ×2.

FIG. 29. Cupule with numerous lobes. B.M., V.42478. ×2.

Sporae dispersae

(All figures are ×500. Locality and horizon same as for the macrofossils.)

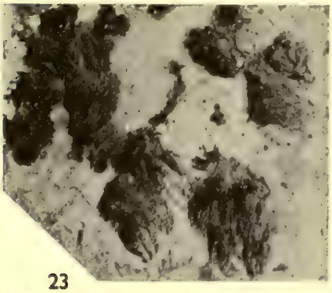
FIGS. 30, 31. *Leiotriletes sphaerotriangulus* (Loose). V.43723, V.43705.

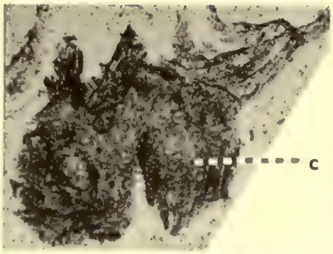
FIGS. 32–34. *Punctatisporites minutus* Kos. V.43721, V.43706, V.43707.

FIGS. 35–37. ? *Punctatisporites minutus* Kos. V.43706, V.43707, V.43713.

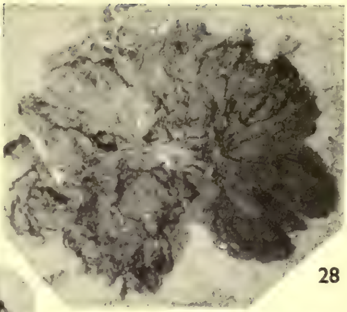
FIGS. 38–42. *Punctatisporites subobesus* sp. nov. (Holotype : Fig. 40). V.43700, V.43720, V.43701, V.43722, V.43726.

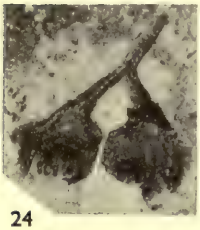
FIG. 43. *Punctatisporites* sp. V.43709.

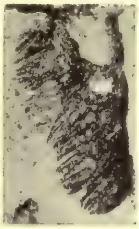

23

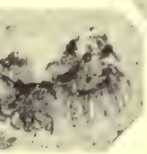


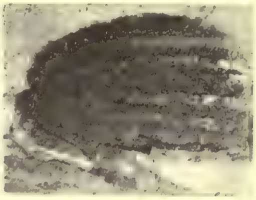
27

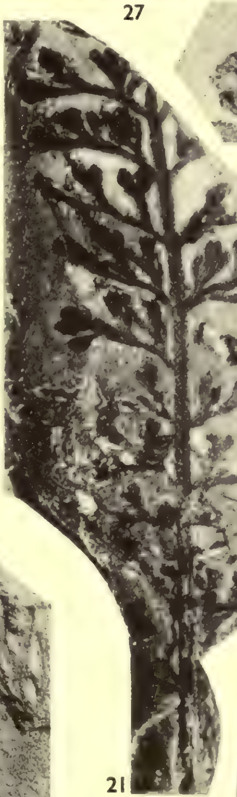

28

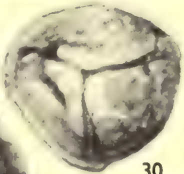

24

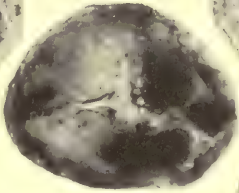

25

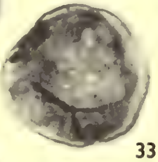

26

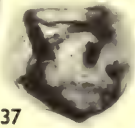

29

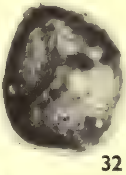

21

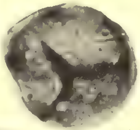

30

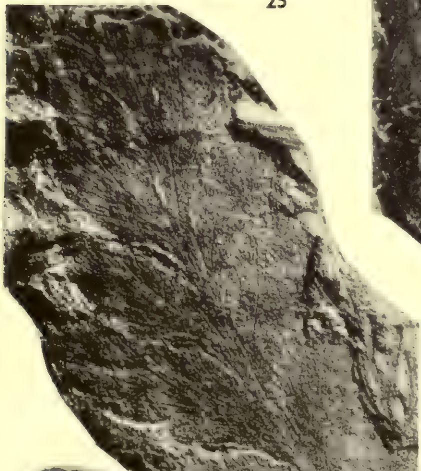

31

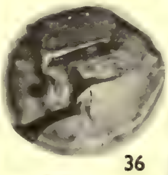

33

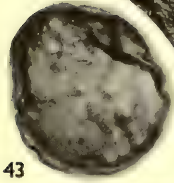

37

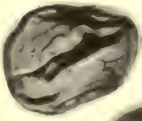

32

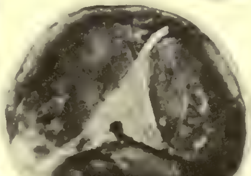

34

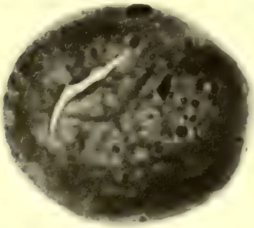

22

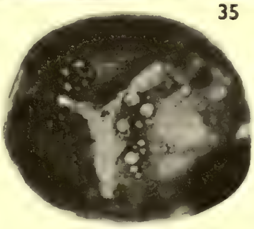

36

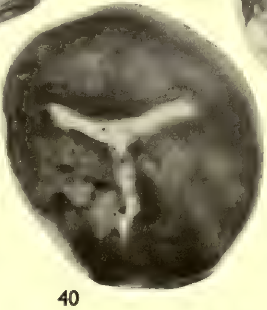

43


35


41


38


39


40

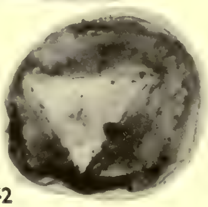
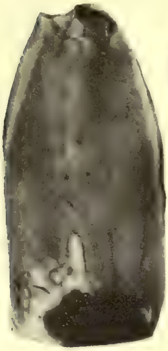
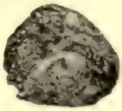

42

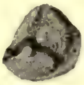
PLATE 22

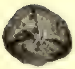
All figures × 500

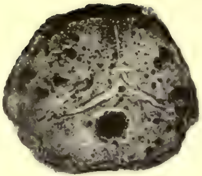
FIG. 44. *Calamospora* sp. cf. *C. mutabilis* (Loose) V.43707.
FIG. 45. *Granulatisporites tenuis* sp. nov. Holotype. V.43708.
FIG. 46. *Granulatisporites tenuis* sp. nov. V.43714.
FIGS. 47, 48. *Granulatisporites* sp. cf. *G. orbiculus* (Pot. & Kr.). V.43702, V.43708.
FIGS. 49–51. *Cyclogranisporites amplus* McGregor. V.43704, V.43721, V.43707.
FIG. 52. *Cyclogranisporites* sp. V.43705.
FIGS. 53–55.—*Planisporites minimus* McGregor. V.43705, V.43711, V.43712.
FIG. 56. *Planisporites* sp. cf. *granifer* (Ibr.). V.43724.
FIG. 57. *Verrucosisporites* sp. V.43716.
FIG. 58. *Camptotriletes* sp. V.43701.
FIG. 59. Cf. *Convolutispora* sp. V.43700.
FIGS. 60, 61. *Microreticulatisporites* cf. *cribellarius* (Horst). V.43710, V.43707.
FIGS. 62, 63. *Microreticulatisporites* spp. V.43703, V.43708.
FIG. 64. *Dictyotriletes* sp. V.43726.
FIG. 65. *Lycospora* cf. *bracteola* Butt. & Will. V.43707.
FIGS. 66–69. *Lycospora* spp. V.43710, V.43715, V.43708.
FIGS. 70, 71. *Anulatisporites anulatus* Pot. & Kr. V.43707.
FIG. 72. ? *Anulatisporites* sp. V.43724.

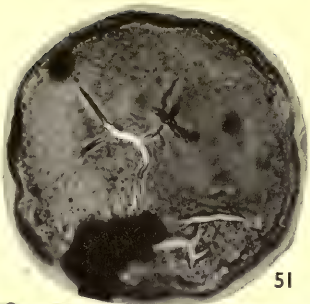

44

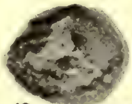

47

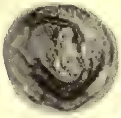

45

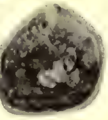

46

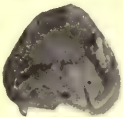

50

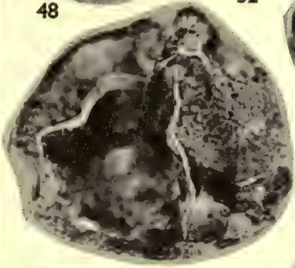

51

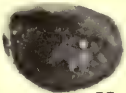

48

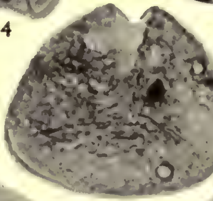

52

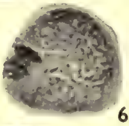

53

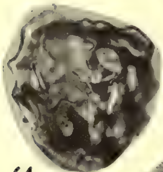

54

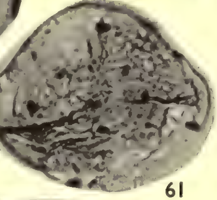

49

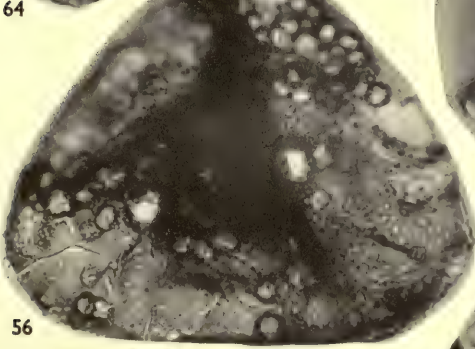

55

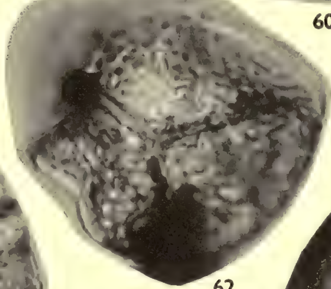

60

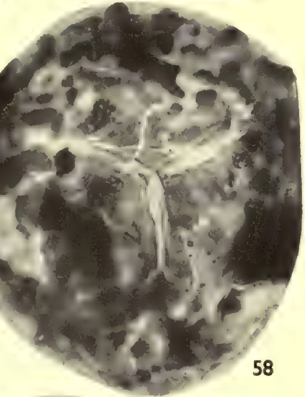

63

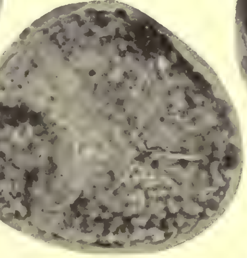

64

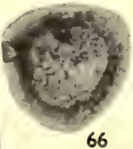

61

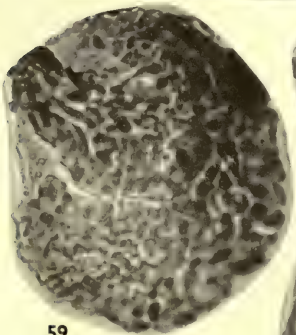

56

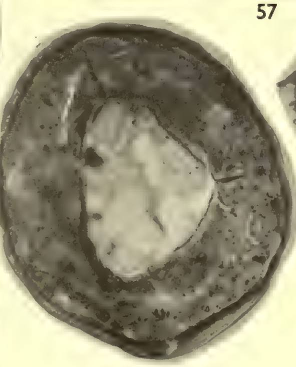

62

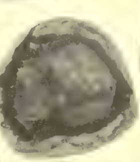

58

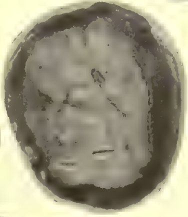

57

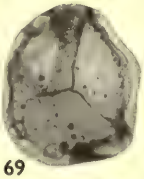

66

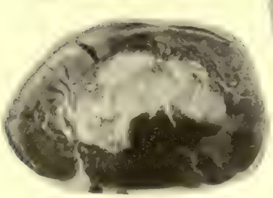

59

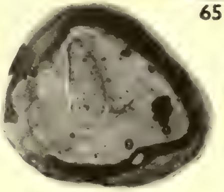

72

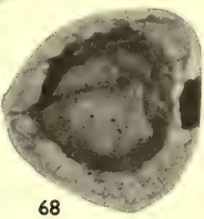

67


65


69


70


71


68

LELE & WALTON

PLATE 23

All figures × 500

FIG. 73. *Densosporites* sp. V.43720.

FIG. 74. Cf. *Cirratriradites* sp. V.43700.

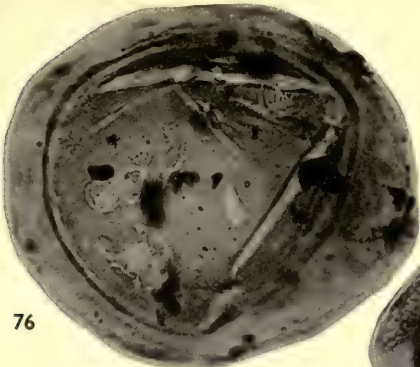
FIG. 75. *Endosporites* sp. V.43727.

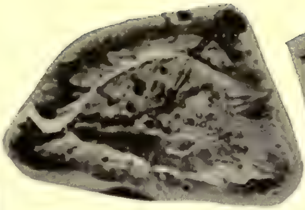
FIG. 76. *Remysporites drybrookensis* sp. nov. Holotype. V.43719.

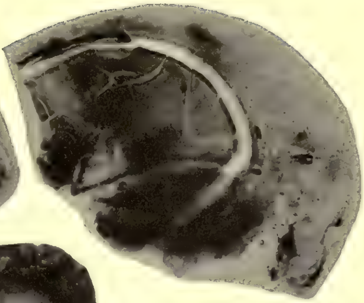
FIGS. 77–81. *Remysporites drybrookensis* sp. nov. V.43725, V.43713, V.43728, V.43717, V.43718.

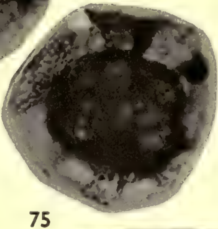
FIG. 82. Cf. *Remysporites* sp. V.43700.

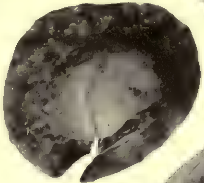
FIGS. 83, 84. *Insertae sedis.* V.43705, V.43711.

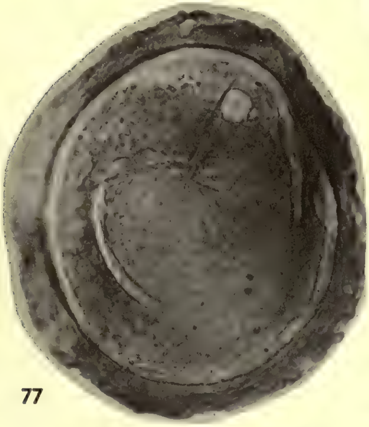

76

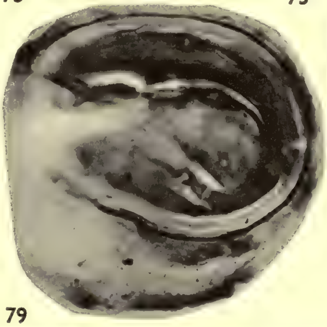

74

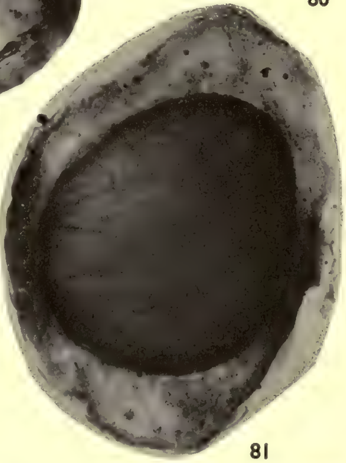

80

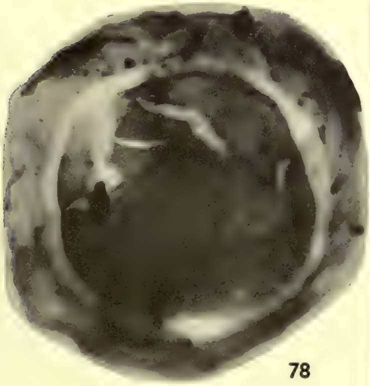

75

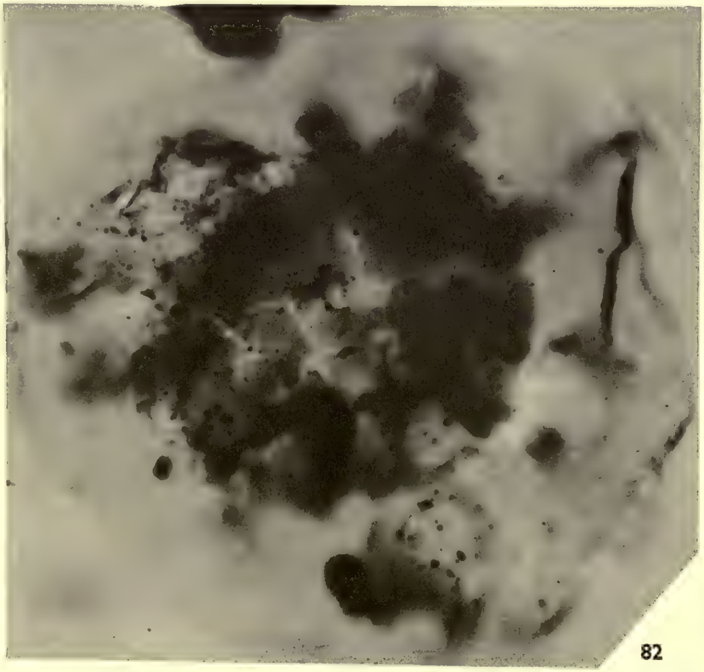

73

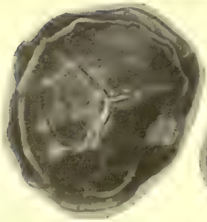

77

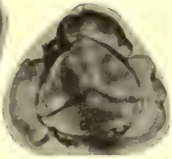

79


81


78


82


84


83

17 AUG 1962
NATURAL HISTORY

PRINTED IN GREAT BRITAIN BY
ADLARD AND SON, LIMITED
BARTHOLOMEW PRESS, DORKING

FOSSIL INSECTS FROM THE LOWER LIAS OF CHARMOUTH, DORSET

F. E. ZEUNER

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 7 No. 5
LONDON: 1962

FOSSIL INSECTS FROM THE LOWER LIAS OF CHARMOUTH, DORSET

BY

FREDERICK EVERARD ZEUNER

Pp. 153–171 ; *Pls.* 24–27

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 7 No. 5
LONDON: 1962

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series, corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

This paper is Vol. 7, *No.* 5 *of the Geological (Palaeontological) series.*

© Trustees of the British Museum 1962

PRINTED BY ORDER OF THE TRUSTEES OF
THE BRITISH MUSEUM

Issued August, 1962 *Price Twelve Shillings*

FOSSIL INSECTS FROM THE LOWER LIAS OF CHARMOUTH, DORSET

By FREDERICK EVERARD ZEUNER

SYNOPSIS

The paper discusses the environmental conditions prevailing in the Lower Lias of England with particular reference to the insect faunas contained in the sediments. It also discusses the degree of salinity insects can withstand. The environment of the Lias is compared with that of the Bombay coast of today, with its numerous islands and inlets, and mud sedimentation.

The new fauna from Charmouth, with six dragonflies, one orthopteron and three beetles, is described. The dragonflies all belong to the almost extinct Anisozygoptera and are among the largest known. The orthopteron belongs to the almost extinct Prophalangopsidae, being their most primitive representative and linking them with the Gryllacrididae. Of the beetles, one is a Cupedid, a member of a family that flourished in the late Palaeozoic ; the two others are of unknown affinities. The structure and coloration of the elytra are analysed and interpreted in detail, providing information about the process of fossilization. The taxonomic status of the two species of *Holcoëlytrum* is discussed and types are designated.

I. GENERAL PALAEOBIOLOGICAL CONSIDERATIONS

An important collection of fossil insects has recently been made by Mr. J. F. Jackson from the " Flatstones " and related deposits near Stonebarrow, Charmouth, on the Dorset coast. The preliminary classification of the specimens, which have been acquired by the British Museum (Natural History), has shown that both in the composition of the fauna and in the preservation they resemble those of the Lower Lias of Gloucestershire, Warwickshire and Worcestershire, though there are some significant differences. Conditions of life, death and fossilization were evidently somewhat similar. In detail, however, several problems arise when the faunal association is studied. Some insects, for instance, including a dragonfly (In. 49573), rest directly on or are closely associated with ammonites.

According to Mr. Jackson (written communication) the following ammonites occur in the deposit : *Asteroceras obtusum*, *Xipheroceras dudressieri*, *Xipheroceras* sp., *Promicroceras planicosta*, very abundant. Fishes are present also and, according to Mr. Jackson's observations, mostly found where plant remains occur. The following species have been recorded : *Dapedium granulatum*, *Dapedium* sp., *Pholidophorus* sp. and *Chondrosteus* sp. (very rare).

Lamellibranchs are rare, except *Inoceramus*, and gastropods are absent. Plants, apart from driftwood, are also rare.

This list of fossils indicates salt-water, with tolerable living conditions in the water itself, whilst conditions on the sea-floor appear to have been unsuitable for many groups one might normally expect to be present. The environment would thus have been essentially marine, and there is a contradiction in the presence of numerous insects together with a marine fauna. The first possibility requiring consideration is that sea-water was less saline in Jurassic times than it is at the present day. An assessment can be made with the aid of Conway's important paper

(1943). From his data it can be calculated that the salinity of the Jurassic ocean was of the order of 3·0%,[1] in other words only slightly less than the ocean of the present (3·4%).

Since British Liassic insect faunas contain fair numbers of species which pass their larval lives in water, the resistance of insects to sea-water needs consideration. Some Apterygota are able to stand temporary submergence and to float on the water of rock pools which are their ordinary environment. A collembolon, *Lipura maritima* L., lives on the shores of Britain ; it is frequent for instance at Selsey in Hampshire on the quiet surface of pools. Another species of the same order, *Actaletes neptuni* Giard, lives on the coast of France where it is temporarily submerged by the tide. But since Apterygota have not yet been recorded from the British Lias, these forms merely indicate possibilities of adaptation. Of greater interest are certain species of Diptera, the larvae of which live on decaying organic matter in jetsam accumulations. They withstand frequent wetting and temporary submergence. A few Diptera are known from the Lias,but nothing is known about their larval modes of life.

There are, however, two important groups with aquatic larvae, the adults of which are well represented in the British Lias, the dragonflies (Odonata) and the caddisflies (Trichoptera). Both are known to occur in brackish water, and their presence in the Baltic Sea has received some attention.

Leander (1901) gave a list of the insects occurring in the sea-water west of Helsinki, Finland. He quoted twenty-one species, comprising one mayfly, nine caddisflies, two bugs, three mosquitoes (two *Chironomus*, one *Ceratopogon*) and six water beetles. These species were found among the islands and associated with the jelly-fish, *Aurelia aurita*, the worm, *Nereis diversicolor*, the barnacle, *Balanus improvisus*, the bivalve, *Cardium edule*, and others. This mixture of freshwater insects and marine species exists in water with about 0·5% of salt.

Silfvenius (1905) reported on the caddisflies found at the entrance of the Finnish Gulf at Tvärminne. The water contains 0·5–0·6% of salt, and no fewer than twenty-four species of caddisflies live in it as larvae, six of them being abundant. It is noteworthy that the bladder-wrack, *Fucus* sp., serves both as food for the larvae and as building material for their cases.

Ussing (1918) studied the insects of the Randers Fjord in Denmark, in which the concentration of salt decreases inland. He found the following :

Salt content	Insects present
Surface 1·7% Depth 2·4%	*Chironomus* larvae only.
Surface 1·2% Depth 1·9%	One dragonfly, 1 water bug, 4 water beetles, 1 leaf beetle, *Chironomus*.
Surface 0·5% Depth 1·3%	Two caddisflies, 1 dragonfly, 1 bug, 4 water beetles, 2 leaf beetles, *Chironomus*, 1 moth.
Surface 0·14% Depth 0·16%	Insect life abundant.

---

[1] Almost the same value is obtained, whether the calculation is based on sodium or on the total of chlorides.

This evidence shows that insect life does not altogether shun salt water, although at concentrations over 0·2% very few species are able to exist, chief among them dragonflies, caddisflies and *Chironomus* mosquitoes. Only the caddisflies, however, have gone some way towards adapting themselves to this environment, as shown by the use of *Fucus* as food as well as building material.

The Recent examples given can be supplemented by a Miocene locality (Zeuner, 1938), the *Hydrobia* Limestone of the Mayence Basin. The brackish character of the water may here be suspected, though not proved, by the abundance of the gastropod *Hydrobia* sp.[1]. The analysis of the insect fauna presents the following picture:

Terrestrial and flying individuals .	139
Aquatic individuals . . .	More than 8

The aquatic individuals comprise two adult water beetles and larvae of Hydrophilidae, two larvae of dragonflies, and larvae of Diptera (Stratiomyidae). Though the larvae have not all been studied, their total will remain small. This particular fauna, from Mombach, differs, in the scarcity of aquatic larvae, from neighbouring localities in which whole beds are composed of the cases of caddisfly larvae. Locally, therefore, and at certain times, the water was inhabited by enormous numbers of these insects. Even at Mombach, however, where no caddis cases have been found, adult caddisflies comprise 50% of the fauna. Adding to these the dragonflies, being aquatic as larvae, and the larvae of the Hydrophilidae and Stratiomyidae, the total of insects dependent on water rises to 63%. This composition suggests that at Mombach the water itself was only partially inhabitable, and this for certain insects only, whilst at other places in the neighbourhood the water must have harboured an abundance of insect larvae. It suggests that the salinity of the lake in which the *Hydrobia* Limestone formed was near the upper limit of concentration bearable by insects, and that in the immediate vicinity enough fresh water, possibly from springs, was available. Such diversity of local biotopes, not evident from the study of the embedding sediment, is by no means exceptional.

On the shore of the Dead Sea in Jordan, for example, a few freshwater pools are fed by springs, as at 'Ain Feshka. They support fishes (*Cyprinodon sophiae, C. cypris, C. dispar*). Only about 10 ft. of beach gravel separates these fishes from the deadly brine of the sea, and on this beach the writer found dead water beetles and locusts. If this combination of species occurred in a fossil context, one would almost certainly credit the Dead Sea with a fish fauna, with insects living in its water as larvae, and with other insects living in the neighbourhood. It is this complexity of the local biotopes that makes the environmental interpretation of fossil insect faunas somewhat difficult. The identification of groups with special environmental requirements and the relative frequency of individuals in the various environmental groups is, however, of considerable use as shown by the examples here quoted.

The Liassic deposits of the south-western Midlands have yielded a fauna which may be regarded as representative of woodlands interrupted by water readily inhabitable by insects. Dense vegetation on the water's edge is suggested. The presence of water of a salinity approaching that of the sea cannot be excluded, but there must have been plenty of accumulations of water less saline than 0·2%, to enable the abundant fauna of caddisflies, dragonflies and others to rear their larvae. The presence of humid ground is indicated by a group of crickets which appears to be related to *Pteronemobius*, and which burrows in moist ground near puddles of water under the surface. Many other Orthoptera Saltatoria are conspicuous in this fauna, the Prophalangopsidae being an almost exclusively Jurassic family which appears to have been living among leafy vegetation. The Panorpoid Complex is well represented, apart from caddisflies, by the Orthophlebiidae, the larval environment of which is unfortunately not yet known.

---

[1] The Oligocene of the Rhine Rift is rich in salt deposits, and the partly saline character of the *Hydrobia* Limestone was first suggested by Wenz (1921), though he was not using evidence based on insects.

Turning now to the insect fauna of the Charmouth Lias, of which 434 specimens are known, it is noteworthy that no aquatic larvae have so far been discovered. Adult caddisflies, too, are completely absent. Among the remainder, the beetles (38·1%) and the Saltatoria (20·8%) dominate. Other groups are represented in small numbers only. These are the Panorpoid Complex (3·2%), Odonata (2·5), Rhynchota (2·5%) and Blattodea (1·8%). 31·1% cannot be classified without further detailed work, and many of these are too poorly preserved to be of interest. If one compares this list with the brackish faunas quoted above, it becomes clear that the insects of Charmouth are at least predominantly derived from another environment, and that their life cycles were not dependent on the water in which they were embedded and which, presumably, was too saline.

Furthermore, the numerical distribution of insect groups in the Charmouth fauna is clearly a function of their resistance to mechanical disintegration. This is why beetles are conspicuous. With them must be ranked the bugs which have hard bodies and, to a lesser extent, the cockroaches. Wings of dragonflies also are resistant to decay in water, and, unlike specimens from the Lias of the Midlands, no bodies have been bound.

The fragile forms belong to the grasshoppers and to the Panorpoid Complex. The former are often very poorly preserved ; many wings are folded over as if by a changing water current. But there are a number of legs, and a few specimens appear to be almost complete with body. This group, therefore, is rather better preserved than the remainder. Apart from the single specimen of *Protohagla langi* sp.n., which is a Prophalangopsid, the great majority of other Saltatoria (if not all) belong to the Elcanidae. This well-known Jurassic family had enlarged spines on the hind tibiae with which it was able to swim, the body being held on the water by surface tension and cutaneous fat, whilst the hind tibiae were dipped into the water, serving as oars.[1] The Elcanidae, which are the ancestors of the Tertiary and Recent Tridactylidae which live on the edge of water and are likewise able to swim, were relatively fragile insects. Their abundance implies that the shore was not far away, and that the surface was not often disturbed by wave action. Salt water would not have affected them.

The Panorpoid Complex from Charmouth contains several groups, Neuroptera, Mecoptera (of which *Orthophlebia* is represented) and Diptera. In addition, there is a solitary Hymenopteron of the sawfly type. All these are poorly preserved, and their number may increase as the undetermined remainder is studied. They provide further evidence that the Charmouth insects had undergone transport and decay before they were embedded in the sediment.

---

[1] First noted by Handlirsch (1908), phylogenetic relations discussed by Zeuner (1938).

Whilst this is obvious even from the condition of many Elcanidae, the more resistant beetles bear it out in an interesting manner. There are many isolated elytra, though bodies, with or without elytra, are not rare. Legs and other appendages are lost without exception. The condition of the Coleoptera is in this respect reminiscent of those found in present-day jetsam, in which they dry out periodically, acquire some buoyancy and are thus washed away and re-deposited several times. Jetsam sedimentation of insects has been described by Trusheim (1929), Schwarz (1939) and Zeuner (1938 : 151). These authors agree that off-land winds play an important part in such formations.

In the Charmouth Lias, jetsam is not likely to have been the cause of the presence of insects. If so, there should be evidence in the form of belts of concentrated fragments of vegetation mixed with marine forms as well as insects. The state of preservation of the present material does not support this idea.

Since the sediment must have been a calcareous mud deposited near land, the possibility of direct wind transport of insects on to wet mud-flats at low tide has to be mentioned. It was so in the case of the Solnhofen Limestone of Upper Jurassic age (Abel, 1929 ; Zeuner, 1939 : 20). Under such conditions, whole insects are often blown on to the flats, where they remain stuck, unable to rise again. They are thus not infrequently embedded in positions indicating their struggle to free themselves. That this interpretation does not apply to the Charmouth Lias is evident.

There remains the possibility of flotsam, of prolonged drifting and slow sinking, followed by incorporation in soft calcareous and bituminous mud, under either tidal or non-tidal conditions. Drifting is partly suggested by the fragmentary condition of most of the insects, though this may be due to other causes such as attack by predators. There is, however, conclusive evidence for extreme water-logging. Several of the beetles are compressed dorsoventrally, which is possible only when they were softened by prolonged wetting and decay. Elytra are often flattened, though by no means always, and they show wrinkles which were produced as the flattening proceeded under the weight of the freshly forming sediment. Furthermore, the wing of *Petrophlebia anglicanopsis*, a dragonfly to be described later in this paper, has its margin characteristically frayed as in modern insect wings that have begun to decompose in water.

These observations favour the interpretation of the insects as flotsam, as indeed does the composition of the fauna. The same can be applied to the Midlands Lias, but there the percentage of fragile insects is so much higher, and the abundance of caddisflies so suggestive of less saline conditions that the environment cannot have been precisely the same.

In the light of the evidence cited from other localities and of the observations made on the material from the Midlands Lias and that of Charmouth respectively, the following deductions may be made concerning the environment. In both areas, mud sedimentation occurred under protected conditions and proceeded in the virtual absence of wave action. The marine fauna may be regarded as implying that tides were present, and there are plenty of present-day areas of sedimentation that fulfil these conditions, especially on the mangrove coasts of the tropics. Those known to the writer are on the coast of Bombay and the Gulf of Cambay. The coast north of Bombay is particularly suitable for comparison. There are numerous low islands which, going inland, fuse into strips of land interrupted by numerous water inlets of varying width. These, in turn, link up with rivers which reduce the salinity of the water until, some 20 miles inland, it is fresh. Mud sedimentation under quiet tidal conditions can be observed in many places. Where tested, the mud is both calcareous and rich in organic matter. Dense vegetation on the islands and the shores harbours a rich fauna of insects, and marine species penetrate as far inland as decreasing salinity will permit them to go. In such an area, one would place the Charmouth Lias among the islands near the open sea, and the Midlands localities within the inlets.

The complete description of the fauna from Charmouth will require considerable time, partly because the poor state of preservation imposes a heavy strain on the eyes of the investigator, and partly because the fragments require large-scale comparison with more complete material from a great variety of insect orders. In this first descriptive part, all the remains of Odonata are described and referred to six species, three of which are new. In addition, the new Prophalangopsid orthopteron is described because of its phylogenetic interest, together with three species of beetles.

2. SYSTEMATIC DESCRIPTIONS

Order *ODONATA*

Suborder ANISOZYGOPTERA Handlirsch

Diagnosis. Nodus placed at great distance from the base of the wing.

Distribution. Mainly Jurassic, with two Recent species.

Family Liassophlebiidae Tillyard

Emended diagnosis. Tillyard's definition (1925 : 11) has now to be modified in so far as the discoidal cell of the fore wing is sometimes closed basally.

Distribution. So far known from the British Lias only, with two genera containing nine species (including those here described for the first time).

Genus ***PETROPHLEBIA*** Tillyard (1925 : 11)

Type species. *Petrophlebia anglicana* Tillyard.

Petrophlebia anglicanopsis sp. n.

(Pl. 24, figs. 1, 2)

Diagnosis. Hind wing with CuA_2 less curved than in the type species, and with indistinct distal portion.

MATERIAL. The holotype, British Museum (Nat. Hist.) In. 49573, Jackson Coll., (Pl. 24, fig. 1) with counterpart; and a second specimen, In. 59376, from the same locality, with counterpart (Pl. 24, fig. 2).

LOCALITY. Lower Lias, Flatstones, Stonebarrow, Dorset.

PARTS KNOWN. Portion of hind wing, and ? apex of wing.

DESCRIPTION. The holotype is a fragment 34·5 mm. long, and 15 mm. wide. It thus belongs to a large species. From the preserved portions of M_4, Cu, and Cu_2 a total length of about 80 mm. can be computed. This is more than in *P. anglicana* as estimated by Tillyard. The principal new specimen is part of a hind wing, seen from the upperside. This has been ascertained from the condition of Cu_1, which is negative (depressed), whilst Cu_2 is a positive (raised) vein.

The venation leaves no doubt that this is a *Petrophlebia*, and this is confirmed by the pretty colour pattern (not mentioned by Tillyard) produced by a dusky pigmentation present along all the cross-veins.

Fragments of R and all branches of M are preserved, but of no particular interest. The area between M_4 and Cu_1 and Cu_2 is narrower towards the apex. The long middle portion of Cu_2 is remarkably straight compared with the type species and it disappears suddenly in the reticulated cross-venation, whilst in *P. anglicana* it can be traced as running in a curve down to the hind margin. The hind margin itself is not preserved.

REMARKS. This fragment (Pl. 24, fig. 1) shows, oddly enough, about the same portion of the wing as does the type species, so that a close comparison is possible. It reveals the differences mentioned; they make a specific separation necessary. The new species, *P. anglicanopsis*, is nevertheless closely related to the type species.

The holotype of *P. anglicanopsis* is partly covered by a fragment of an ammonite, probably *Asteroceras obtusum* (J. Sowerby). The marine context of sedimentation is thus evident, and the poor condition of the wing, with its corroded edge, suggests prolonged drifting.

The second specimen is tentatively referred to this species, though it shows some resemblance to *Diastommites liassina* (Strickland). It will be necessary to study the affinities of this species with care, as it may prove to be closely related to *Petrophlebia*.

Genus ***LIASSOPHLEBIA*** Tillyard (1925 : 13)

TYPE SPECIES. *Liassophlebia magnifica* Tillyard (1925 : 14).

REMARKS. Apart from the type species, Tillyard included in this genus one species first described by Hagen (1850) as *Heterophlebia westwoodi* and later (Hagen, 1866) transferred to *Tarsophlebia*. This assignation was accepted by Handlirsch; it established the relationships of the entire family subsequently erected by Tillyard.

Tillyard further described three new species. Two new species are described in the present paper, and some additional information concerning the type species is provided. There is, in addition, a fragment which cannot be assigned to a species with certainty, though it clearly belongs to the genus.

Liassophlebia magnifica Tillyard

(Pl. 27, fig. 1)

1925 *Liassophlebia magnifica* Tillyard, p. 15, pl. 1, fig. 3; pl. 2, fig. 4; text-figs. 3, 4.

MATERIAL. British Museum (Nat. Hist.), In. 64000 (Pl. 27, fig. 1), In. 59106 and In. 49213, all from The Flatstones, Stonebarrow, Charmouth, Dorset. All with counterparts.

EMENDED DESCRIPTION. Tillyard's description and illustration of the anal area of the hind wing (poorly preserved in the holotype) can be improved with the aid of In. 64000, which shows the details with unusual clarity (Pl. 27, fig. 1). Most important, there is an anal angle after all, and as sharp as in most Anisoptera, as well as a large triangular basal cell, into which a short, blindly-ending cross-vein protrudes from A. Tillyard was right in suspecting that the subquadrangle contained a group of three cross-veins, which he dotted in his text-fig. 4, except that the third, which points downwards, does not join up with another vein, but ends blindly. A similar " blind end " protrudes into the discoidal cell. The basal vein of the subquadrangle continues quite straight beyond this structure down to the posterior angle of the wing.

REMARKS. This is the only dragonfly species common to both the Charmouth and the Midlands Lias.

Liassophlebia jacksoni sp. n.

(Pl. 25)

DIAGNOSIS. Hind wing with 14 postnodals.

HOLOTYPE. British Museum (Nat. Hist.), In. 53999, with counterpart. Jackson Coll., the only specimen.

LOCALITY. Lower Lias: Flatstones, Stonebarrow, Charmouth, Dorset.

PARTS KNOWN. Hind wing only, portion beyond pterostigma not preserved.

DESCRIPTION. As for *Progonophlebia* from the Lias of Gloucestershire (Zeuner, 1958), this description and those that follow use exactly the same venational nomenclature as Tillyard (1925). It will thus be possible to compare the species and identify material. It does not, however, imply that I am in agreement with Tillyard regarding the names given to certain veins. The matter, which raises the problem of the crossing of tracheae in the immature wing, is too complicated to be discussed here and requires further studies not only of Recent material but of fossils.

Total length of hind wing about 83 mm. (computed value; 67 mm. preserved). This compares with 70 mm. in *L. magnifica*. Greatest width, 28 mm., compared with 21 mm. in *L. magnifica*.

Pterostigma not fully preserved, basal side apparently vertical. Nodus situated nearer the base than the tip of the wing. Fourteen postnodals (only 10 in *L. magnifica*). Subquadrangle traversed by one strong vein, which is concave towards the apex.

M_{1A} weak, reduced to a short length, and joining M_2. More distad, the two veins separate again. This condition is confirmed by the counterpart specimen. Oblique vein between M_2 and M_S present and situated below the seventh postnodal. Between

M_4 and Cu_1, distad of the triangle, four rows of cells (only two in *L. magnifica*). Base of wing with straight vertical vein as in *Aeschna*. Dark pigmentation at the base in two distinct patches, one on Sc + R, the other on Cu.

REMARKS. This species is much larger than *L. magnifica* Tillyard, described from Warwickshire, and several of the venational characters are in keeping with this, as they strengthen the large wing.

The size of the wing has been computed in the following way. If the distance from the nodus to the pterostigma is used as a basis for the calculation, the total length would amount to 83·5 mm. On the other hand, if the width is used, assuming proportions similar to those of *L. magnifica*, the wing would have been 93 mm. long. This is improbable, since the preserved length between nodus and pterostigma should then be longer than it actually is and contain even more than 14 postnodals. Thirdly, assuming the proportions of both species to be the same and using the distance from nodus to pterostigma, one arrives at 78 mm. This is too short, for the postnodal section of the new species is proportionately longer than the antenodal. Thus, the most likely length is 83·5 mm., and it emerges that the new species is much broader then *L. magnifica*. If it had the same length/width ratio as this species, it should be only 25 mm. broad instead of 28 mm. as measured. It is safe, therefore, to regard the size given in the description as approximately correct. The insect must have presented a magnificent sight, with its wing-span of between 7 and 8 inches, when flying over the estuaries of Liassic Charmouth.

The difference in pigmentation, compared with the type species, confirms that the Charmouth species cannot be a large individual of the Warwickshire species.

The new species is named after Mr. J. F. Jackson of Charmouth, the indefatigable collector of Dorset fossils. *Liassophlebia jacksoni* is the seventh species of the genus to be described. The genus must have been flourishing in the British Lias, and it is curious that it has not yet been found elsewhere.

Liassophlebia gigantea sp. n.

(Pl. 27, fig. 2)

Diagnosis. Very large *Liassophlebia* with cross-vein linking Cu with arculus in fore wing so as to form a triangle.

HOLOTYPE. British Museum (Nat. Hist.), In. 51030, with counterpart. Jackson Coll., the only specimen.

LOCALITY. Lower Lias: Woodstones, Black Ven, Charmouth, Dorset.

PARTS KNOWN. Basal portion of fore wing.

DESCRIPTION. Two very strong antenodals (called "hypertrophied" by Tillyard in other species). From these and from the width between C and Cu the length of the wing can be calculated. The former index gives 82 mm., the latter 84 mm. for the fore wing. The size of this species, therefore, must have been about the same as that of *L. jacksoni*.

The arculus is continued by an exceptionally strong vein on the distal side of the discoidal cell. This vein is approximately at right angles to the long axis of the wing; in fact, it is very slightly turned back. In *L. magnifica*, it is distinctly turned forwards.

It is also distinguished by a cross vein which connects Cu with the arculus, whilst in *L. magnifica* the discoidal cell is open at the base.

From *L. withersi* Tillyard (which is a much smaller species) it is distinguished by the same characters, except that *L. withersi* also has a closed discoidal cell. The closing cross-vein is, however, much nearer to the base of the wing.

Remarks. Though identical with *L. jacksoni* in size, this specimen has very much thicker veins. It is for this reason that it is here regarded as a distinct species.

Liassophlebia sp.

Material. British Museum (Nat. Hist.), In. 53972, with counterpart. Jackson Coll.

Locality. Lower Lias : Flatstones, Stonebarrow, Charmouth, Dorset.

Description. A fragment of C, Sc and R of a hind wing as far as the nodus, and traces of M and Cu. Length from first antenodal to nodus, 23·5 mm.

Remarks. The two "hypertrophied" antenodals prove that this is a *Liassophlebia.* The fragment appears to have suffered much from softening in water, for there are two unusual features difficult to explain as genuine venational elements, viz., the C is depressed between the two antenodals, and basad of the second antenodal Sc and R seems to be fused. It is inadvisable, therefore, to assign this fragment to a particular species, though it is likely to belong to one of them.

Family ARCHITEMIDAE Handlirsch

Genus ***DIASTATOMMITES*** Handlirsch (1920 : 178)

For status of family and genus, see Tillyard (1925).

Diastatommites liassina (Strickland) ?

(Pl. 27, fig. 3)

1840 *Aeshna liassina* Strickland, p. 301, fig. 11.
1856 *Diastatomma liasina* (Strickland) Giebel, p. 276.
1906 *Diastatomma liasina* (Strickland) : Handlirsch, p. 465.
1925 *Diastatommites liassina* (Strickland) : Tillyard, p. 23.

Material. One specimen, British Museum (Nat. Hist.), In. 59375, with counterpart, from the Lower Lias : Flatstones, Stonebarrow, Charmouth, Dorset. Jackson Coll.

Remarks. I refer this small fragment to *Diastatommites* with considerable hesitation. It appears to be the anal portion of a hind wing. If so, Cu_2 is exceptionally strongly curved. It is to be hoped that more and better material will be discovered which would help also to clear up the uncertainty regarding the systematic position of this genus.

Length of the fragment, 22 mm.

Three other tiny fragments of dragonfly wings, In. 49247 (Stonebarrow), In. 53895

(Black Ven) and In. 59109 (Stonebarrow), may be mentioned to complete the record. They are unidentifiable.

Order *ORTHOPTERA SALTATORIA*

Suborder ENSIFERA

Family PROPHALANGOPSIDAE Caudell

Subfamily HAGLINAE Zeuner

Genus ***PROTOHAGLA*** nov.

DIAGNOSIS. A Prophalangopsid whose male elytra have almost straight longitudinal veins, except for CuP and 1A, which are regularly concave towards the fore margin.

TYPE SPECIES. *Protohagla langi* sp.n. (only species).

Protohagla langi sp. n.

(Plate 26)

DIAGNOSIS. Male fore wing broadest at end of basal third. Total length of fore wing about 67 mm. (61 mm. preserved). Maximum width 26 mm. Pattern of four dark cross-bands, most pronounced in the anterior portion of wing. Hind wings appear to exceed fore wings in length.

HOLOTYPE. British Museum (Nat. Hist.), In. 59018, with counterpart. Jackson Coll., the only specimen.

LOCALITY. Lower Lias: Flatstones, Stonebarrow, Charmouth, Dorset.

PARTS KNOWN. Basal two-thirds of fore wing, distal portion of hind wing.

DESCRIPTION. Fore wing very large, length about 67 mm., of which 61 mm. are preserved, maximum width 26 mm. In spite of this, the venation is slightly simpler than in other genera. Four dark cross-bands form a conspicuous colour-pattern of the fore wing. The tip of the hind wing also appears to have been darkened.

Precostal area well developed and separated from the rest of the fore margin by a conspicuous long C. The outline of the part resembles that of *Tettigonia viridissima* L. Sc extending over about five-sixths of the fore margin; it has 14 branches.

R separated from Sc by a field of densely-spaced parallel cross-veins, area between R and Rs similar, but wider, with at least three branches, the first of which is independent as in *Hagla*. Rs with at least four, possibly five, branches.

M separated from R by an area of densely-spaced parallel cross-veins at right angles to the longitudinal veins, but between Rs and M they are oblique.

M three-branched, as in the female of *Hagla*, MA being a simple fork, whilst MP begins with a short oblique stalk, is fused with CuA for some distance, and then free again. The free portion is almost straight and undivided.

Cu consisting of a forked CuA, an unbranched Cu_n, and an unbranched CuP, as in

Hagla. It differs, however, from that of *Hagla* in that *both* Cu_n and CuP branch off before the junction with MP (in *Hagla* Cu_n distad, see Zeuner, 1939, pl. 26, figs. 2, 3). Cu_n is slightly concave towards the fore margin, CuP pronouncedly so. The areas between CuA and Cu_n, and between Cu_n and CuP, are thus broadest in the middle.

Of 1A, only the basal and distal portions are preserved. It is strongly concave towards the fore margin near the base and, if a line in the third fifth of the area between CuP and 1A is correctly interpreted as part of the latter vein, slightly bent towards the fore margin in this zone. This would give it a somewhat wavy run, though one very much less intense than in *Hagla*.

The anal area being damaged, 2A, 3A and Ax (if present) cannot be seen.

The hind wing is folded and lies beneath the fore wing. It appears to have exceeded the latter in length, for its tip is darkened. The traces of veins that can be discerned call for no comment.

DISCUSSION AND REMARKS. This magnificent fossil is remarkable in several respects. From the point of view of preservation it is evident that both fore and hind wing were nipped off simultaneously at the base, and the victim was not then flying. Considering how detached the movements of the wings of Saltatoria are whilst in flight, they must have been tightly closed at the time when the insect was being dismembered. This makes one think of a predator that caught it over the land, rather than of a dragonfly catching a flying insect over the water. What sort of predator this may have been is guesswork for the time being; perhaps it was a flying reptile.

In general appearance *Protohagla* must have resembled *Tettigonia* rather than *Prophalangopsis*, or perhaps more still one of the large tropical Phaneropterinae with irregularly-veined fore wings and long hind wings, such as *Zeuneria* sp.

The affinities of *Protohagla* are with *Hagla*, a well-known genus from the British Lias. The simple venation of *Protohagla* might at first sight suggest that the specimen is a female, but the inverted run of Cu_n, CuP and 1A clearly indicates modifications in the direction of those observed in the males of *Hagla*, where the peculiar kink in these veins foreshadows the way in which the stridulating organ of the later Prophalangopsidae and Tettigoniidae was to evolve. In the females of *Hagla* these veins are unspecialized and convex towards the fore margin.

Protohagla langi is the most primitive Prophalangopsid so far known, though not the oldest, *Notopamphagopsis bolivari* Cabrera from Argentina being of Triassic age. *Protohagla* is an important phylogenetic link with the Gryllacrididae, of which *Jurassobatea gryllacroides* Zeuner from the Upper Jurassic of Solnhofen, Bavaria, shows several features reminiscent of the fore wing of *Protohagla*, especially CuP, 1A and 3A being bent in a similar manner, and the cross-venation being parallel, not reticulated. The new genus thus connects the Prophalangopsidae more closely with the Gryllacrididae, the most primitive family of all Saltatoria Ensifera.

The species is dedicated to Dr. W. D. Lang, F.R.S., who first recommended to me the insects of the British Lias as a subject worthy of study. That he was right in regarding them as such is borne out by the many descriptions that have appeared in the last thirty-five years, as well as by Mr. Jackson's discoveries at Charmouth, with which Dr. Lang is closely connected.

Order *COLEOPTERA*

Family CUPEDIDAE

Genus ***LIASSOCUPES*** nov.

DIAGNOSIS. Cupedid with rounded pronotum.

TYPE SPECIES. *Liassocupes parvus* sp. n. (only species).

Liassocupes parvus sp. n.

(Pl. 27, fig. 4)

DIAGNOSIS. As for genus.

HOLOTYPE. British Museum (Nat. Hist.), In. 64008. Jackson Coll., the only specimen.

LOCALITY. Lower Lias : Flatstones, Black Ven, Charmouth, Dorset.

PARTS KNOWN. Elytra, pronotum, head.

DESCRIPTION. The specimen is a well-preserved beetle, but unfortunately the distal part of the elytra is missing. The elytra must have been about twice as long as the preserved portion.

Width of beetle across elytra, 2·6 mm., preserved length of elytra, 4·0 mm., pronotum, 1·9 mm.

The elytra show the dense regular network of longitudinal ridges with numerous cross-connections characteristic of the Cupedidae. On the assumption that this beetle had the same slender shape as Recent *Cupes*, they should have been long and parallel-sided. There are eight or nine longitudinal lines in the network, of which the fourth is distinctly stronger, another Cupedid feature. In life this fossil must have resembled the Recent *Cupes capitatus* Fabr. of North America in general appearance.

The pronotum and head lie directly in front of the elytra, tilted at an angle of 135 degrees to the right, evidence of severe water-logging. The pronotum is almost circular and shows no spines or other details. It is narrower than the pair of elytra, and this is again another Cupedid characteristic.

The head is poorly preserved, but its granular surface is discernible, the mandibles can be recognized and the head is inserted horizontally in front of the pronotum. No spines or protuberances can be seen, and the antennae are not preserved.

REMARKS. The shape of the pronotum and the exceptionally small size are characteristic. Its sculpture distinguishes this species from the fragment recently described by Gardiner (1961 : 87) as *Metacupes harrisi*, from the Rhaetic of Bridgend, Glamorgan.

Family ?

Genus ***HOLCOËLYTRUM*** Handlirsch (1906 : 453)

DIAGNOSIS. Beetles with elytra with conspicuous black and white longitudinal stripes.

TYPE SPECIES. *Holcoëlytrum giebeli* Handlirsch, 1906, by monotypy.

Distribution. Lower Lias of England.

Remarks. The two species described by Handlirsch as *Holoëlytrum giebeli* and *Holcoptera schlotheimi* are unlikely to belong to different genera. The holotypes of both are reported to have been incorporated in the British Museum, but only that of the first species is known. It is unwise, therefore, to use the second as the type species. The holotype of *Holcoëlytrum giebeli*, though only a fragment of an elytrum, is recognizable, so that this species defines the genus satisfactorily. It is, incidentally, by far the more common species. For lack of generic differences, *Holcoptera* is therefore here regarded as a synonym of *Holcoëlytrum*, which genus now contains the two species easily distinguishable as follows :

(1) Elytrum about 12 mm. long, with 5 black stripes . . *Holcoëlytrum giebeli* Hdl.
(2) Elytrum about 5 mm. long, with 4 black stripes . . *Holcoëlytrum schlotheimi* (Hdl.)

Holcoëlytrum giebeli Handlirsch

(Pl. 27, figs. 6–8)

1845 (Harpalideous Carabidae) Brodie, pp. 101, 124, pl. 10, fig. 2.
1856 *Harpalus Schlotheimi* Giebel, p. 63. (*Partim.*)
1906 *Holcoëlytrum Giebeli* Handlirsch, p. 453, pl. 41, fig. 64.

Diagnosis. Elytrum over 10 mm. long, with five black stripes.

Distribution. Lower Lias of England.

Holotype. British Museum (Nat. Hist.), I. 3581. Brodie Coll. Probably from Apperley, Gloucestershire.

Material. In addition to the holotype, forty-three specimens from the Flatstones of the Lower Lias of Charmouth, Jackson Coll., as follows :

(a) *Stonebarrow, Charmouth, Dorset*

Bodies with both elytra, with counterpart : In. 51002 (Pl. 27, figs. 7, 8), 53928, 53937 ; three specimens.

Single elytra, with counterpart : In. 49204, 43981, 49563, 49229, 49570, 49227, 49611, 49228, 53989, 53962, 49239, 53985, 49585, 59129, 59141, 59134, 59153, 59117, 64013, 64012, 59145, 49244, 64009 ; twenty-three specimens.

Single elytra without counterpart : In. 64010, 64011, 49149, 53943, 49219, 53974, 49610, 49616 (Pl. 27, fig. 6), 59148, 59138 ; ten specimens.

(b) *Black Ven, Charmouth, Dorset*

Single elytra with counterpart : In. 49209, 59100, 48163, 49621 ; four specimens.

Single elytra without counterpart : In. 49619, 49211, 59393 ; three specimens.

Total, forty-three specimens.

Parts known. Elytra, scutellum, tip of abdomen (In. 53928), fragment of leg (In. 53937).

Description. No complete beetles have so far been found. The three specimens with pairs of elytra look broader and stouter than they would have appeared in life, since they are dorsoventrally compressed, causing the elytra to gape at the distal end. Size and shape are comparable with a large *Tenebrio molitor* L., or with *Feronia* sp. The scutellum is very small, and the fragments of abdomen and leg present no features worth mention. In. 51002 shows the underside of the body (on the counterpart), in addition to the striped elytra (Pl. 27, fig. 8).

The elytra are noteworthy for their longitudinal stripes. In the diagnosis they have been given as black. Alternatively, the unpigmented interstices can be counted. There are at first sight four of them. The outer (anterior) margin of the elytron also is represented by a pale line (In. 49616). Counting this as Line 1, one finds that Nos. 1 and 2 are joined near the apex, continuing as a single line for a short distance and ending free within the black. Also, Nos. 3 and 5 are similarly joined, without continuation. They thus enclose No. 4. All are bent towards the shoulder near the base and towards the apex at the distal end. It is evident that these lines represent the veins, whilst the black lines are the interstices. The veins represented are Sc (Line 1), R, Rs, M, and Cu, on the interpretation given to the elytral ridges of the Cupedidae by Zeuner (1933 : 294).

The question arises whether the veins were ridges in the elytra. They could equally well have been immersed within the elytron. A break between the upper and the lower cuticles would result in the same structure on the rock surface as would be produced by ridges.

Some specimens show only three black stripes, the inner and the outer being absent. In these cases, the white lines are broader than usual. One may be inclined to regard these as a different species, but In. 53981 demonstrates conclusively that both variants are merely aspects of the same type of elytron. In the specimen mentioned part and counterpart have five and three black stripes respectively. Unfortunately, this specimen is much flattened. On the counterpart, the anterior edge is distinctly bent upwards, as it is in a large number of Recent beetles. It may thus be presumed that the three-striped aspect is the lower (or underside) of the elytron. This is confirmed by one of the few specimens that have retained some of their original curvature. In specimen In. 49611 the surface is distinctly convex, identifying this as a left elytron. Its colourless lines are very distinct on the counterpart, which is the negative of the upper surface. Since they are wider on the lower part, they must represent lumina in the elytron. It is highly probable, therefore, that these elytra had five ridges corresponding to the major longitudinal veins, and that the membrane between the veins was pigmented black.

One further detail is supplied by In. 49616, and less clearly by others. There is a concentration of black along the white lines, whilst the central portions of the dark stripes are grey. It appears that the latter were thinner than the sides of the ridges. This is as it should be if the ridges contained tracheal lumina.

Having ascertained the structure of the elytron, it is now possible to describe it in some detail.

Elytra 11·8–13·5 mm. long, and up to 4·0 mm. wide (less originally, since flattened *post mortem* ; 3·5 mm. normal). Black, with four prominent ridges corresponding to R, Rs, M, Cu. These and the anterior edge (Sc) usually colourless in the fossils which are split between the upper and lower membranes. Sc and R joined distad, with a short single continuation, Rs and Cu likewise joined distad but not continued. M inside the area enclosed by Rs and Cu, without touching them. On specimens showing the veins as white lines, shoulder portion always black. All veins, except Sc, bent forwards at the base.

REMARKS. Brodie (1845 : 124) regarded this species as " appearing in form nearest to the Harpalideous Carabidae ". Handlirsch refuted this, and its systematic position must remain uncertain until a specimen with head and pronotum is found.

Nevertheless, owing to the five " black stripes " separated by four " white lines ", the species is the most easily recognized among the beetles of the British Lias.

Holcoëlytrum schlotheimi (Giebel)

(Pl. 27, fig. 5)

1845 (Harpalideous Carabidae) Brodie, pp. 101, 124, pl. 6, fig. 28.
1856 *Harpalus Schlotheimi* Giebel, p. 63.
1906 *Holcoptera Schlotheimi* Giebel : Handlirsch, p. 453, pl. 41, fig. 63.

DIAGNOSIS. Elytron over 5 mm. long, with four black stripes.

DISTRIBUTION. Lower Lias of England.

HOLOTYPE. British Museum (Nat. Hist.), I. 3582. Brodie Coll., from Binton, Warwickshire, is supposed to be the holotype. The specimen is labelled as " Carabidae (Harpalideous), Figd. Brodie, Foss. Ins. pl. 6, f. 28, p. 101, 124, Brodie Coll." Except in size, however, it does not agree with the figure referred to, being uniformly black and lacking the stripes. The specimen is marked on the rock itself " Binton ", and on a label glued to it is written " Carabidae Pl. 6, f. 28 " and on the reverse " Harpalideous Carabidae ". This appears to be in Brodie's own handwriting, so that the mistake was made by Brodie himself. The locality given in his book (p. 101) is Apperley or Brockeridge. Since Apperley is the type locality of *H. giebeli*, the type of *H. schlotheimi* should have come from Brockeridge.

It is clear, therefore, that the specimen marked as the type, I. 3582, is not the holotype, and that the true holotype was lost long ago, probably in Brodie's time. For diagnostic characters one has to rely on Brodie's illustration and description, and a Neotype has been selected from the new material.

NEOTYPE. British Museum (Nat. Hist.), In. 59115, from the Flatstones, Stonebarrow, Charmouth, Dorset. Jackson Coll. (Pl. 27, fig. 5).

OTHER MATERIAL. In. 53990 with counterpart, from the same locality.

PARTS KNOWN. Elytra in pairs, parts of prothorax.

DESCRIPTION. Of the two specimens available, In. 59115 shows the same kind of black stripes as *H. giebeli*. There are two in the central part of the elytron, and one thin one along the hind margin. The latter touches the corresponding stripe of the other elytron in the position of rest, so that the beetle appears to have five stripes. The intervening white lines are broader in this species than in *H. giebeli*, and all join the pale anterior margin at the apex. Their bases are bent forward as in the other species. One vein, therefore, is not marked (or atrophied) in *H. schlotheimi*. Most probably R lies close to Sc, the black stripe between them being missing.

The dorsal counterpart of the second specimen (In. 53990) is almost uniformly black, confirming the observations made on the extensive material of *H. giebeli*; but in this specimen the longitudinal ridges are discernible, and there appears to be a fine punctation present on the surface of the elytron

The scutellum and a portion of the prothorax are preserved in In. 53990, without providing diagnostic information.

Elytra 5·5 mm. long, 3 mm. wide.

Remarks. This species is much rarer than *H. giebeli.* There can be no doubt that the two specimens described here belong to *H. schlotheimi,* based on Brodie's figure (1845, pl. 6, fig. 28).

REFERENCES

Abel, O. 1922. *Lebensbilder aus der Tierwelt der Vorzeit.* 643 pp., 1 pl. Jena.

Brodie, P. B. 1845. *A History of the Fossil Insects in the Secondary Rocks of England.* 130 pp., 11 pls. London.

Conway, E. J. 1943. The chemical evolution of the ocean. *Proc. R. Irish Acad.*, London, **48**, B : 161–222.

Gardiner, B. G. 1961. New Rhaetic and Liassic Beetles. *Palaeontology*, London, **4** : 87–89, 3 figs.

Giebel, C. 1856. *Fauna der Vorwelt mit steter Berücksichtigung der lebenden Thiere,* 2, 1. 511 pp. Leipzig.

Hagen, H. 1850. *In* Selys-Longchamps, E. de & Hagen, H. A. Revue des Odonates ou Libellules d'Europe. *Mém. Soc. Sci. Liége,* **6** : xxii + 406 pp., 11 pls.

—— 1866. Hemerabiidarum Synopsis synonymica. *Entom. Zeit.*, Stettin, **27** : 369–462.

Handlirsch, A. 1906–08. *Die fossilen Insekten und die Phylogenie der rezenten Formen.* 1430 pp., 51 pls. Leipzig.

Leander, K. M. 1901. Übersicht der in der Umgebung von Esbo-Lofo im Meerwasser vorkommenden Tiere. *Acta Soc. Fauna Flora fenn.*, Helsingforsiae, **20**, 6 : 1–20.

Schröder, C. 1920. *Handbuch der Entomologie,* **3**. Jena.

Schwarz, A. 1931. Insektenbegräbnis im Meer. *Natur u. Mus.*, Frankfurt, **61** : 453–465.

Silfvenius, A. J. 1905. *Zur Kenntnis der Trichopterenfauna von Tvärminne.* Festschr. J. A. Palmen, **2**, 14 : 1–31. Helsingfors.

Strickland, H. E. 1840. On the Occurrence of a Fossil Dragon-fly in the Lias of Warwickshire. *Mag. Nat. Hist.*, London (n.s.) **4** : 301–303, text-figs. 11–13.

Tillyard, R. J. 1925. *The British Liassic Dragonflies* (*Odonata*). 40 pp., 5 pls. British Museum (Nat. Hist.), London.

Trusheim, F. 1929. Massentod von Insekten. *Natur. u. Mus.*, Frankfurt, **59** : 54–61.

Ussing, H. 1918. Insektlivet i og ved Gudenaaens Delta og Randers Fjord. *In* Johansen, A. C. *Randers Fjords Naturhistorie.* København.

Wenz, W. 1921. *Das Mainzer Becken und seine Randgebiete.* 351 pp., 518 figs. Heidelberg.

Zeuner, F. E. 1933. Die Stammesgeschichte der Käfer. *Paläont. Z.*, Berlin, **15** : 280–311, 14 figs.

—— 1938. Die Insektenfauna des Mainzer Hydrobienkalks. *Paläont. Z.*, Berlin, **20** : 104–159 pls. 13–17.

—— 1939. *Fossil Orthoptera Ensifera.* xiii + 321 pp., 80 pls. British Museum (Nat. Hist.), London.

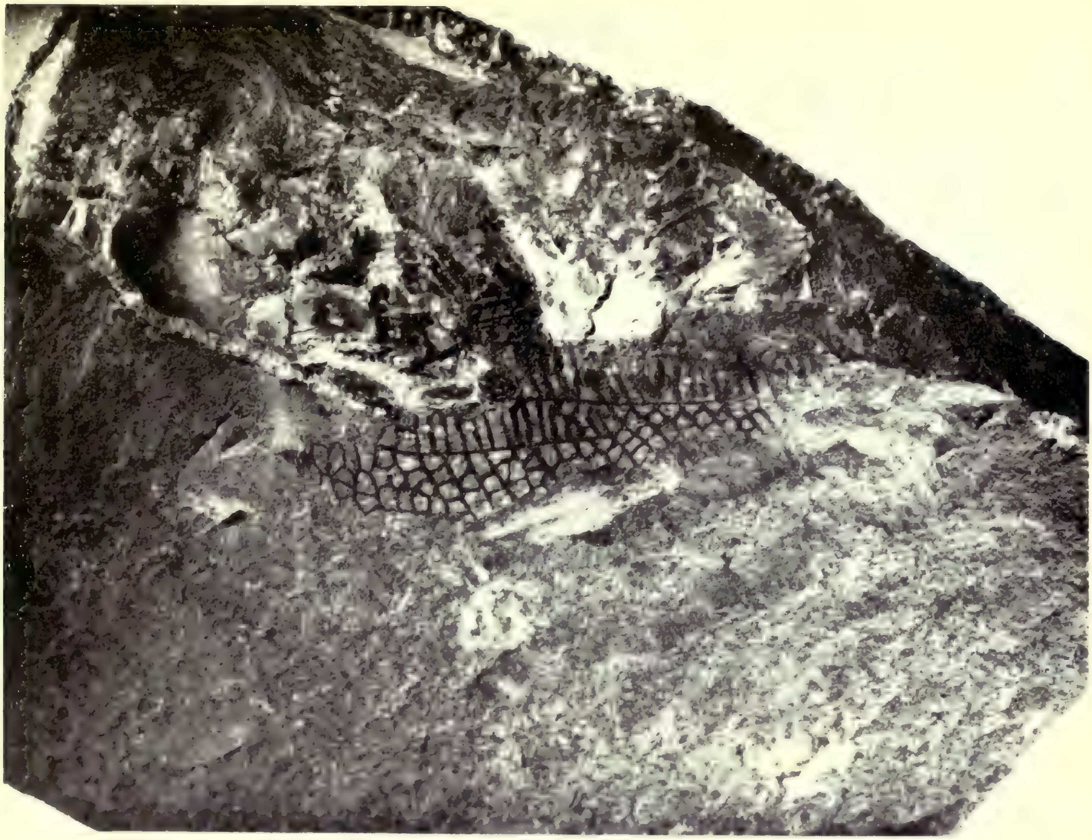
—— 1940. *Saltatoria Ensifera fossilia. Fossilium Catalogus,* **1** : Animalia, Pars 90. 108 pp. The Hague.

—— 1958. A new Liassic Dragonfly from Gloucestershire. *Palaeontology*, London, **1** : 406–407, pl. 72, fig. 4.

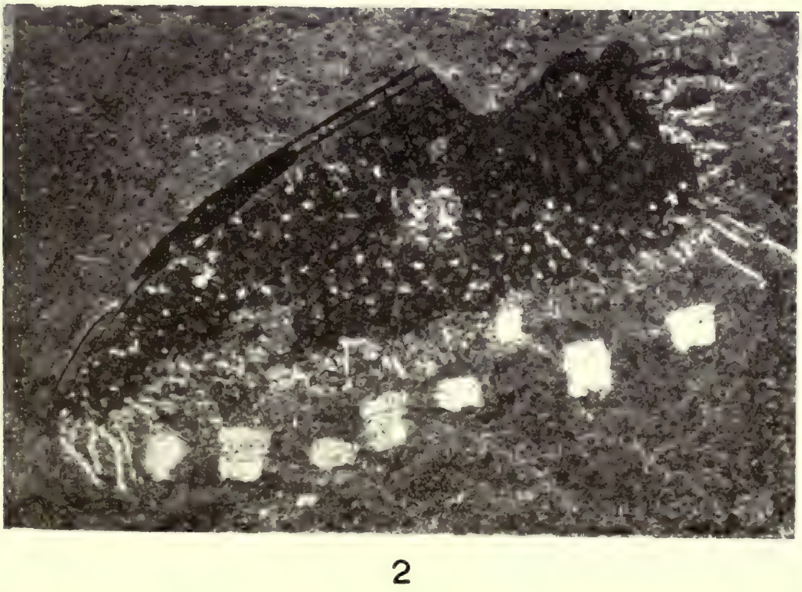
7 AUG

PLATE 24

FIG. 1. *Petrophlebia anglicanopsis* sp. n. Holotype. In. 49573. ×1·85.
FIG. 2. A second specimen doubtfully referred to *P. anglicanopsis*. In. 59376. ×2·2.



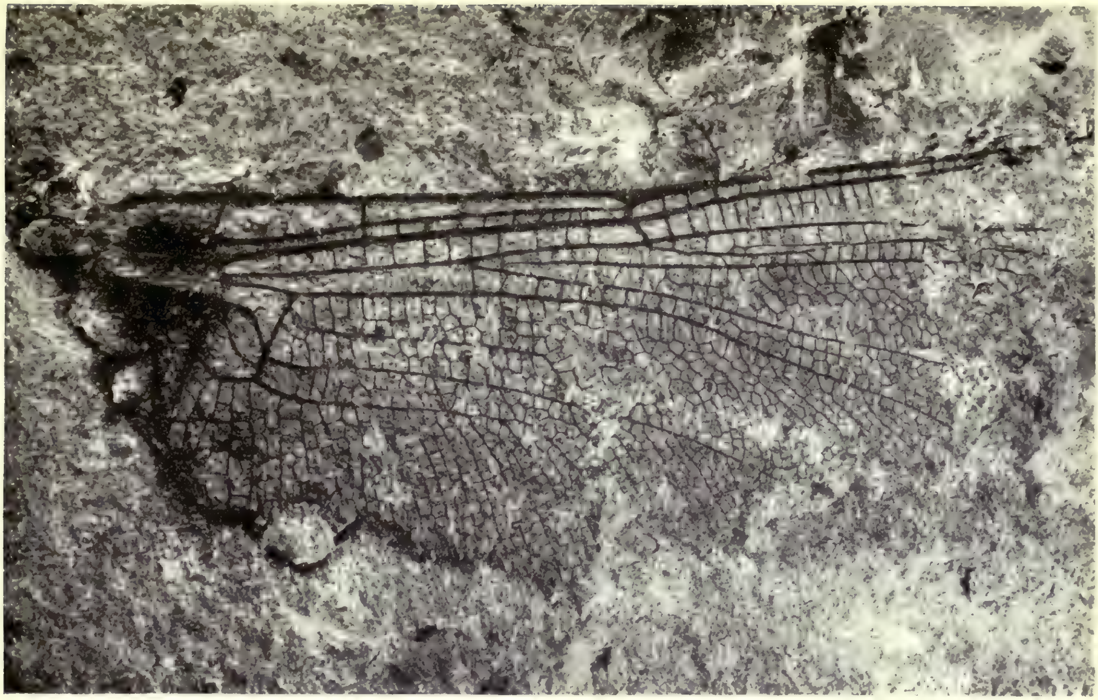
1



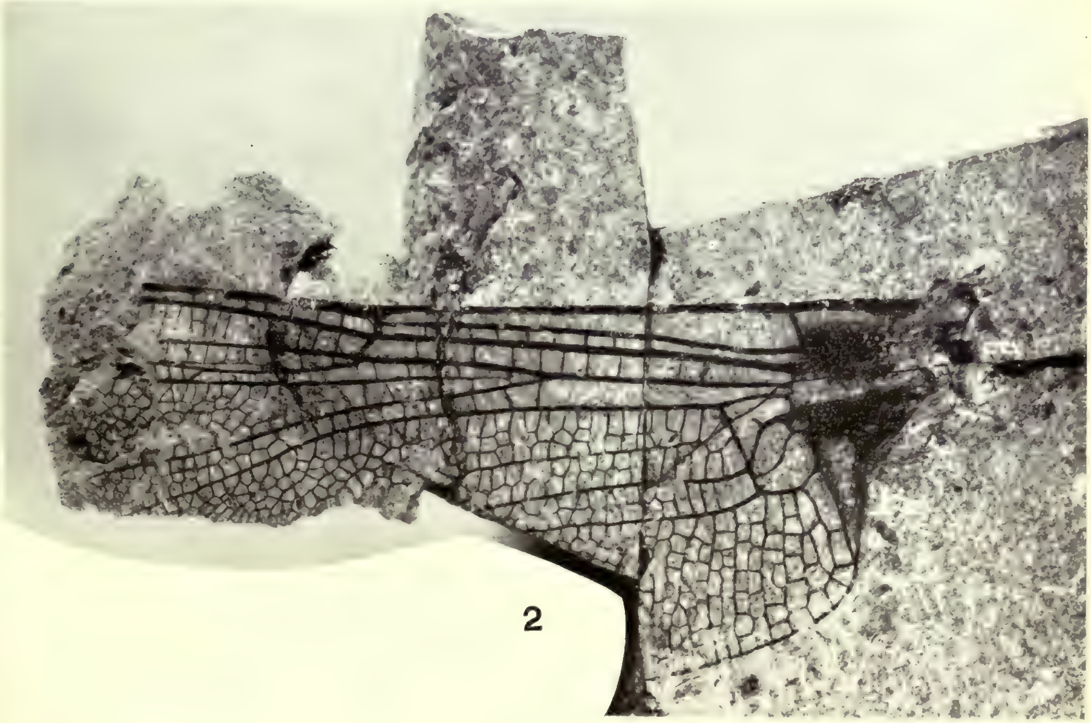
2

PLATE 25

FIGS. 1, 2. *Liassophlebia jacksoni* sp. n. Holotype (Fig. 1) and counterpart (Fig. 2). In. 53999. ×2.



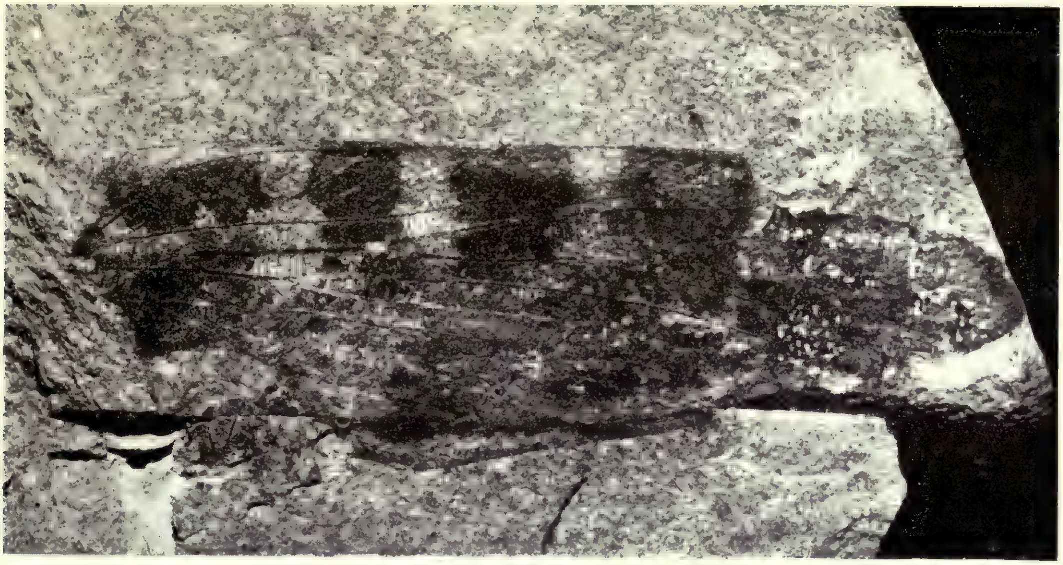
1



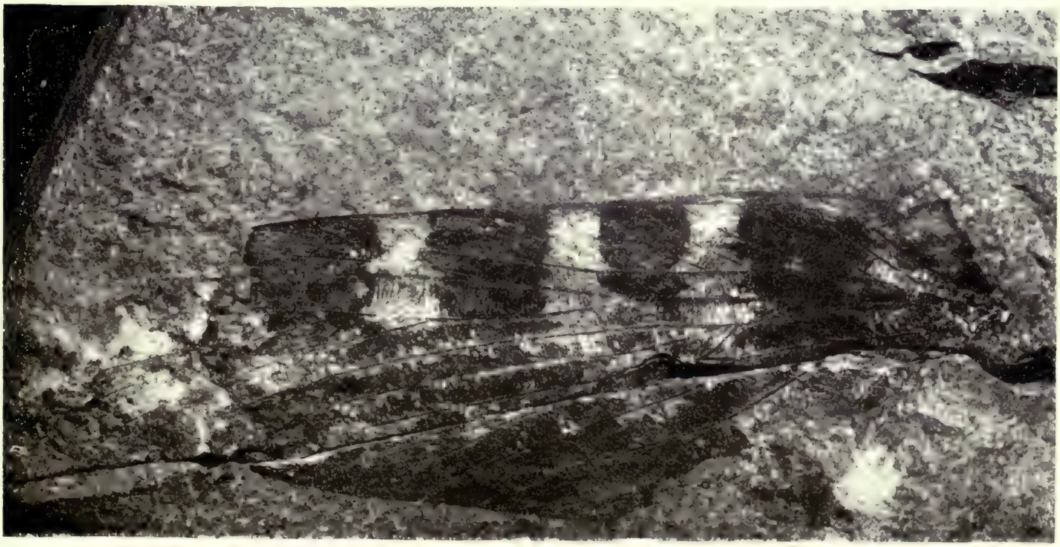
2

PLATE 26

FIGS. 1, 2. *Protohagla langi* gen. et sp. n. Holotype (Fig. 1) and counterpart (Fig. 2). In. 59018. × 1·7 and 1·6 respectively.



1



2

PLATE 27

FIG. 1. *Liassophlebia magnifica* Tillyard. In. 64000. ×2·4.

FIG. 2. *Liassophlebia gigantea* sp. n. Holotype. In. 51030. ×2.

FIG. 3. *Diastatommites liassina* (Strickland) ? In. 59375. ×2.

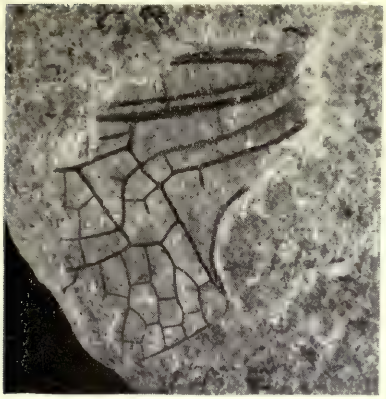
FIG. 4. *Liassocupes parvus* gen. et sp. n. Holotype. In. 64008. ×10. On the right above the pair of elytra lie the pronotum and head, cut off in this print.

FIG. 5. *Holcoëlytrum schlotheimi* (Giebel). Neotype. In. 59115. ×2·9.

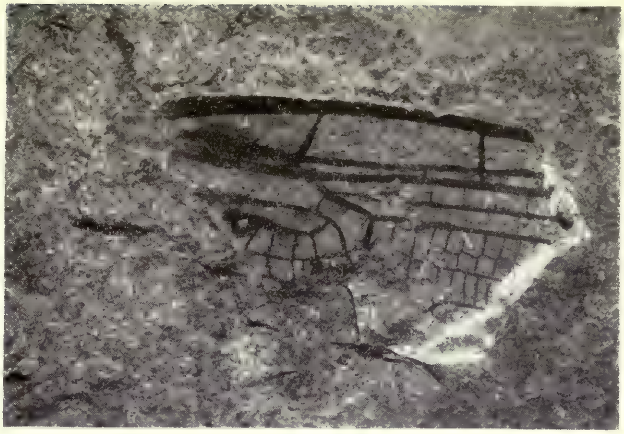
FIG. 6.—*Holcoëlytrum giebeli* Handlirsch. In. 49616. ×3·1.

FIG. 7. *Holcoëlytrum giebeli* Handlirsch. A pair of elytra. In. 51002. ×2·9.

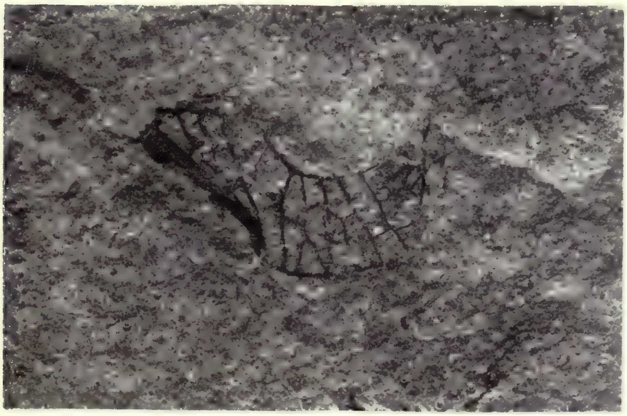
FIG. 8. *Holcoëlytrum giebeli* Handlirsch. Underside of specimen shown in Fig. 7. ×2·9.



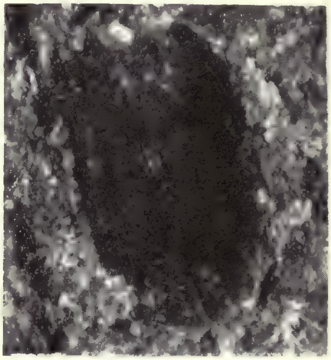
1



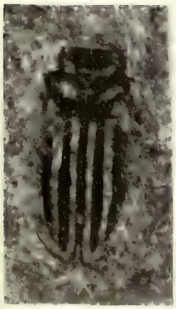
2



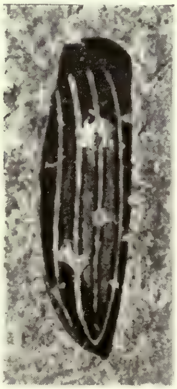
3



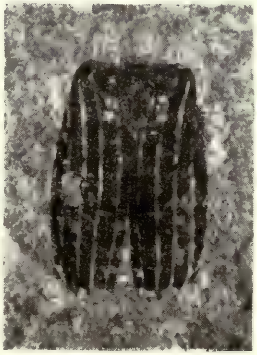
4



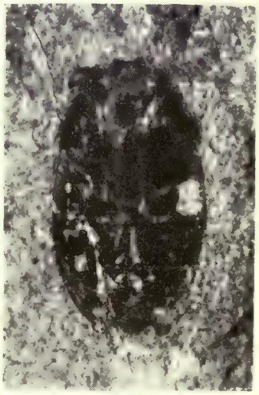
5



6



7



8

PRINTED IN GREAT BRITAIN BY
ADLARD AND SON LIMITED
BARTHOLOMEW PRESS, DORKING

THE ENGLISH CRETACEOUS TURRITELLIDAE AND MATHILDIDAE (GASTROPODA)

1 [illegible] 62

H. L. ABBASS

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 7 No. 6
LONDON : 1962

THE ENGLISH CRETACEOUS TURRITELLIDAE AND MATHILDIDAE (GASTROPODA)

BY

HOUSSEIN LOUTFY ABBASS

Department of Geology, Faculty of Science,
Ain Shamo University, Cairo, U.A.R.

Pp. 173–196; *Plates* 28–32; 19 *Text-figures*

DEC

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 7 No. 6
LONDON: 1962

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series, corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

This paper is Vol. 7, *No.* 6 *of the Geological (Palaeontological) series.*

© Trustees of the British Museum, 1962

PRINTED BY ORDER OF THE TRUSTEES OF
THE BRITISH MUSEUM

Issued December, 1962 *Price Fourteen Shillings*

THE ENGLISH CRETACEOUS TURRITELLIDAE AND MATHILDIDAE (GASTROPODA)

By H. L. ABBASS

SYNOPSIS

The paper is a systematic study of the Turritellidae and other *Turritella*-like gastropods found in the Cretaceous rocks of England. The number of species recognized is 13, of which the following are described as new: *Turritella* (*Torquesia*) *tamra*, *T.* (*Torquesia*) *wagihi*, *T.* (*Torquesia*) *faizai*, *T.* (*Torquesia*) *hassani*, *Turritella* (*s. lat.*) *ageri*, *Turritella* (*s. lat.*) *sherborni*, *Mathilda coxi*, *M. ahmadi*. Formations of Albian age (the Blackdown Greensand and the Gault) have yielded the greater number of the gastropods described, but some species come from the Aptian, Cenomanian, and Senonian.

INTRODUCTION

THE work which has led to the present paper was carried out in 1954–6 in the Department of Geology of the Imperial College of Science, London, in partial fulfilment of the requirements for the degree of Ph.D. of the University of London. The author has received advice and help from several people, and is especially grateful to Dr. L. R. Cox, of the British Museum (Natural History), and to Dr. D. V. Ager, of the Imperial College, in this connection. The material examined belongs to the collections of the Department of Palaeontology of the British Museum (Natural History), the Geological Survey of Great Britain, the Sedgwick Museum (Cambridge), Mr. C. W. Wright, and Dr. J. M. Hancock. The writer tenders his thanks to these two gentlemen and to the authorities of the institutions mentioned for the facilities afforded him to carry out the work.

STRATIGRAPHICAL NOTES

Fossil turriculate gastropods occur in several of the English Cretaceous marine formations. They are, however, known only from a relatively few localities and are rarely abundant, so that there is no possibility of their being used stratigraphically. Most of the material described in this paper comes from old museum collections and in some cases nothing is known of the precise horizons and localities from which the specimens were collected. There is a probability that in some cases specimens with similar labels (e.g. " Gault, Folkestone ") may come from a whole range of horizons within the formation stated.

The marine Neocomian rocks found in Lincolnshire and Yorkshire have yielded no

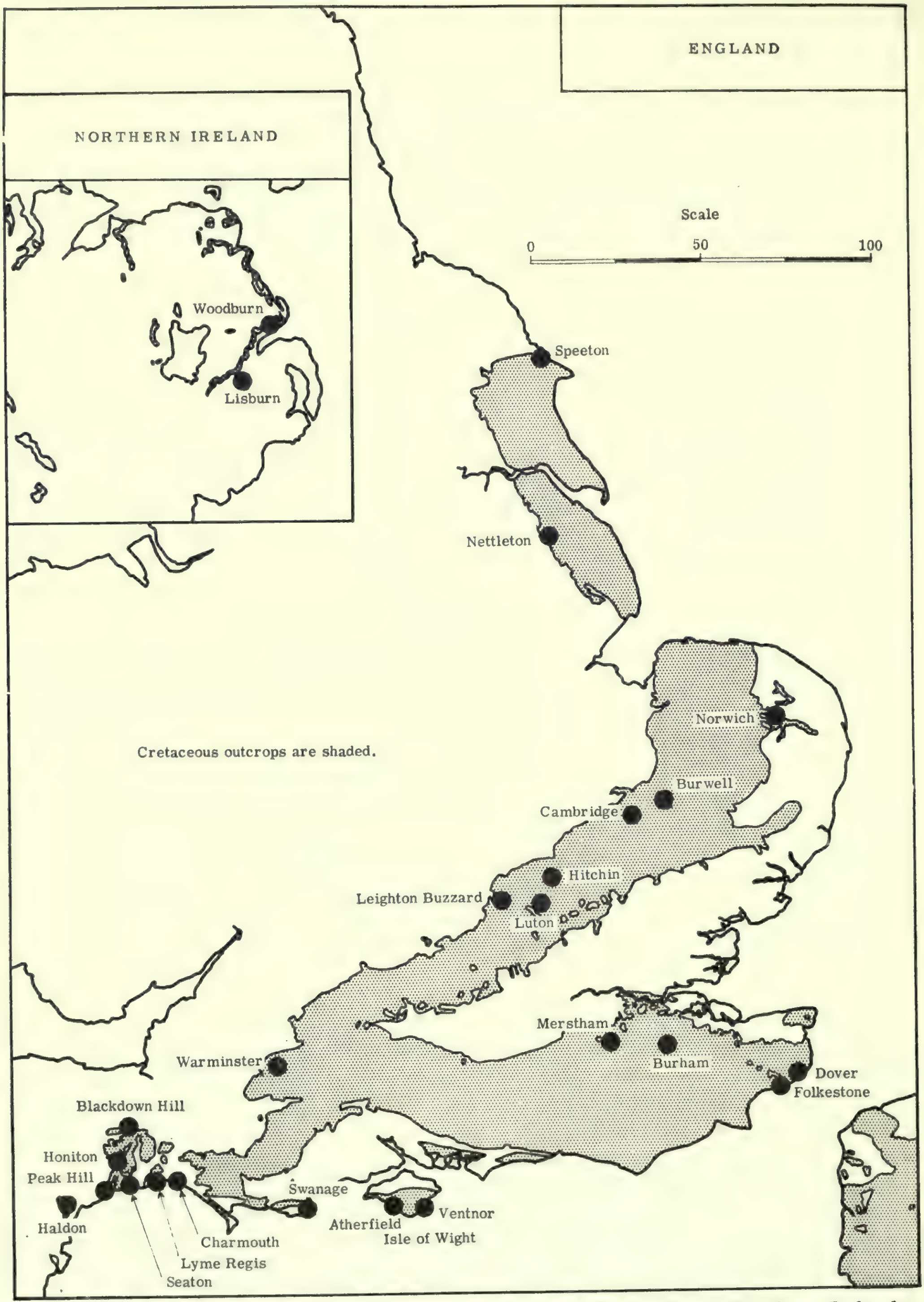

ENGLAND
NORTHERN IRELAND
Woodburn
Lisburn
Scale
0
50
100
Speeton
Nettleton
Cretaceous outcrops are shaded.
Norwich
Burwell
Cambridge
Hitchin
Leighton Buzzard
Luton
Merstham
Burham
Warminster
Dover
Folkestone
Blackdown Hill
Honiton
Peak Hill
Haldon
Swanage
Atherfield
Ventnor
Isle of Wight
Charmouth
Lyme Regis
Seaton

FIG. 1. Sketch map showing the Cretaceous outcrop in England and Northern Ireland, with localities marked.

representatives of the Turritellidae, and the contemporaneous Wealden deposits of south-eastern England are deltaic and lacustrine sediments with fossil gastropods belonging to non-marine genera.

Aptian deposition began in the English area with marine transgressions from the south and north. The isthmus separating the northern and southern basins was eventually submerged in mid-Aptian times, and throughout the rest of the Cretaceous period there was a single basin of deposition in the British area. The Aptian rocks or Lower Greensand of the Weald and other districts of the English mainland have not yielded any of the gastropods described in the present study, but the rich faunas found in the south of the Isle of Wight near Atherfield, where the Lower Greensand reaches its maximum thickness of 800 ft., include members of both the Turritellidae and the Mathildidae. The two species here described, *Turritella* (*Torquesia*) *tamra* sp. nov. and *Mathilda coxi* sp. nov., both come from the rock bands known as the Crackers, belonging to the Atherfield Clay series.

The Albian stage is represented in the Wealden district by the upper part of the Folkestone beds and by the Gault, a stiff clay, the narrow, elliptical outcrop of which occupies low-lying ground between the Lower Greensand hills and the Chalk downs. The thickness of the Gault is variable, being about 300 ft. near Eastbourne and 100 ft. at Folkestone, and at the latter locality its rich fauna includes many gastropods, most of which, however, are more or less crushed. Two species from the Gault of Folkestone, *Turritella* (*Torquesia*) *vibrayeana* d'Orbigny and *Turritella* (*Torquesia*) *wagihi* sp. nov., are described in the present paper, and the first has also been found in the thin deposit of Gault clay found below the Upper Greensand at Charmouth, Dorset. The Greensand of Blackdown, Devon, also of Albian age, is the most prolific source of Cretaceous gastropods in England, and they are silicified and relatively well preserved. The following species from Blackdown are here described: *Turritella* (*Torquesia*) *granulata* J. de C. Sowerby, *Turritella* (*Torquesia*) *faizai* sp. nov., *Turritella* (s. lat.) *ageri* sp. nov., *Turritella* (s. lat.) *sherborni* sp. nov., and *Mathilda ahmadi* sp. nov. The first occurs in great abundance.

The Cenomanian stage is represented by rocks of greensand facies in south-eastern Devon and in the Warminster district of Wiltshire. *Turritella* (*Torquesia*) *granulata* occurs in the Cenomanian of both areas, and a second species, *Turritella* (*Torquesia*) *hassani* sp. nov., in Devon. Except in these two areas, deposition of calcareous marl now represented by chalky rocks had begun by the beginning of Cenomanian times. This change in sedimentation was formerly interpreted as the result of a gradual sinking of the sea-floor that continued, with slight pauses, for a long period over almost the whole area that is now the British Isles. The lack of clastic sediment may, however, have been due to other causes, as the fossils found in the Chalk do not seem to have been deep-sea forms. The Cenomanian chalky rocks of Kent and Cambridgeshire have yielded *Turritella* (*Turritella*) *dibleyi* Newton, and those of Sussex and the Isle of Wight "*Turritella*" *turbinata* J. de C. Sowerby, a large gastropod which belongs most probably to a new genus.

Although rare in the great mass of the post-Cenomanian Chalk, gastropods are relatively abundant in the rock-bands at the top of the Turonian known at the Chalk Rock, but no Turritellidae have been found at this horizon. The Senonian

Chalk of Norwich, however, has yielded the species *Turritella* (*Turritella*) *unicarinata* (S. Woodward), a form also found in the Upper Chalk of northern Ireland.

TABLE I.—*Summary of the Distribution in England of the Species Described*

	Aptian	Albian	Cenoman.	Turon.	Senon.
Turritella (*Turritella*) *dibleyi*			Kent, Cambs.		
,, ,, *unicarinata*					Norfolk
,, (*Torquesia*) *granulata*		Devon	Devon, Wilts.		
,, ,, *tamra*	I. o. W.				
,, ,, *vibrayeana*		Kent, Dorset			
,, ,, *wagihi*		Kent			
,, ,, *faizai*		Devon			
,, ,, *hassani*			Devon		
,, (s. lat.) *ageri*		Devon			
,, ,, *sherborni*		Devon			
Mathilda coxi	I. o. W.				
,, *ahmadi*		Devon			
" *Turritella* " *turbinata*			Sussex, I. o. W.		

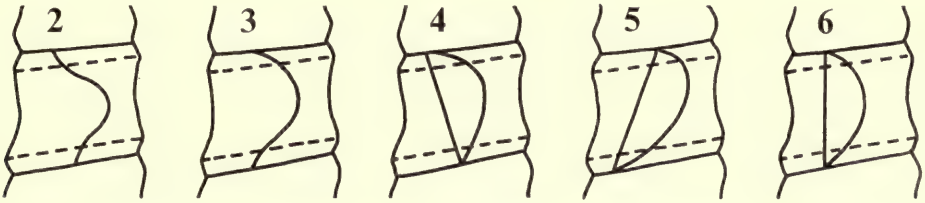
NOTES ON TAXONOMY AND TERMINOLOGY

Of modern authors who have discussed the morphology of the shell in the Turritellidae and the taxonomic value of its various features, particular mention may be made of Cossmann (1906, 1912, 1916), Guillaume (1924), Dollfus (1926), Merriam (1941) and Marwick (1957). All of these workers have pointed out the significance of the form of the growth-lines as seen between successive sutures on the spire whorls, and Marwick has extended the study of the growth-lines to their continuation as seen on the base of the last whorl.

Cossmann, in his review of the family, also took into account the outline and ornament of the whorls and the degree of acuteness of the spire. He recognized three genera with numerous subgenera and sections, and he considered *Turritella* (*Turritella*), *Turritella* (*Zaria*), *Turritella* (*Haustator*), *Turritella* (*Peyrotia*), *Turritella* (*Archimediella*), and *Mesalia* all to be represented in the Cretaceous, *T.* (*Haustator*) by numerous species. The studies of Guillaume were confined to Tertiary forms. This author based his classification entirely on the form of the growth-lines as seen between the sutures, but he did not assign subgeneric names to the groups which he distinguished. Merriam, in his work on the Upper Cretaceous and Tertiary Turritellidae of western North America, paid attention, not only to the growth-lines, but also to the order in which the elements of spiral ornament appear in the early ontogeny of the shell. He recognized a number of distinct lineages but refrained from assigning subgeneric names to them.

Marwick, in his generic revision of the family, considers both the growth-lines and the ontogeny of the primary elements of spiral ornament to be valuable criteria for classification, and he also finds that the nature of the protoconch is of help in this connection. He interprets genera in a more restricted sense than did his predecessors, recognizing 33 in all, distributed among five subfamilies; in addition, he regards nine named taxa as subgenera. The data assembled by Marwick show that the following genera or subgenera have species of Cretaceous age as their types: *Arcotia* Stoliczka (Upper Cretaceous, India), *Colposigma* Finlay & Marwick (Danian, New Zealand), *Craiginia* Stephenson (Cenomanian, North America), *Leptocolpus* Finlay & Marwick (Danian, New Zealand), *Sechuritella* Olsson (Upper Cretaceous, Peru), and *Torquesia* Douvillé (Cretaceous, widespread). The geological ranges of the various genera are not given in Marwick's paper and it is possible that he would consider some of those with Tertiary or Recent type-species to be represented in the Cretaceous.

Owing to the state of preservation of the available material it is seldom possible, when studying Cretaceous specimens, to observe the protoconch, the development of the elements of spiral ornament in early ontogeny, or even the growth-lines on the base of the last whorl. In the present paper, therefore, particular attention is paid to the form of the growth-lines between the sutures, and the taxonomic groups of Turritellidae which are recognized are treated as subgenera of *Turritella*. The forms described include the type-species of *Torquesia* (*Turritella granulata* J. de C. Sowerby), and this subgenus has proved to be suitable for the reception of several other English species. The other taxa mentioned above as being based on Cretaceous species are not represented in the material studied.



FIGS. 2–6. Terminology of growth-lines in Turritellidae.

2. Two points of inflection.
3. One point of inflection.
4. No point of inflection. Growth-line chord prosocline.
5. No point of inflection. Growth-line chord opisthocline.
6. No point of inflection. Growth-line chord orthocline.

Two of the *Turritella*-like species here described have been recognized as representatives of the genus *Mathilda*, the presence of which in the Cretaceous was first recorded by Cossmann. One of these (*M. coxi* sp. nov.) is the earliest known representative of the genus and of the family Mathildidae.

The terminology employed in the present paper is mainly that used by previous students of the Turritellidae. The less familiar terms are explained by Text-figs. 2–6. The *growth-line chord* may be defined as a straight line joining the points where a growth-line meets successive sutures.

Most of the new species are named after geologists and others who have helped the author during the course of the work.

SYSTEMATIC DESCRIPTIONS

Class GASTROPODA
Subclass PROSOBRANCHIA
Superfamily CERITHIACEA Fleming, 1822
Family TURRITELLIDAE Woodward, 1851
Genus ***TURRITELLA*** Lamarck, 1799 : 74

TYPE SPECIES.—*Turbo terebra* Linnaeus, 1758 (by monotypy).

Subgenus ***TURRITELLA*** s. str.

SUBGENERIC CHARACTERS.—Shell medium-sized to large, slender ; whorls evenly convex, ornamented with spiral cords and threads ; growth-lines between sutures forming a simple sinus of no great depth.

Turritella (Turritella) dibleyi Newton

(Pl. 29, figs. 7, 8 ; Text-fig. 7)

1918. *Turritella dibleyi* Newton, p. 97, pl. 10, figs. 1, 2.

HOLOTYPE.—In the British Museum (Natural History), reg. no. G. 29362.

DESCRIPTION.—The shell is moderately large and slender. The apical whorls, up to a diameter of about 9 mm., are missing in the holotype. The whorl outline is rather strongly convex, but in the holotype the convexity of the earlier preserved whorls has apparently been reduced by pressure ; the suture is moderately deep. About 30 spiral threads are present on the spire whorls. They are crossed by collabral threads which tend to become prominent at variable intervals, almost forming varices, and become generally stronger on the later whorls, so that the appearance of collabral ornament is developed in places. The spiral threads are separated by interspaces the width of which is almost equal to that of the threads. The base and aperture are damaged in the holotype. The growth-lines show a broad, shallow sinus with no points of inflection, and the growth-line chord is prosocline (Text-fig. 7).

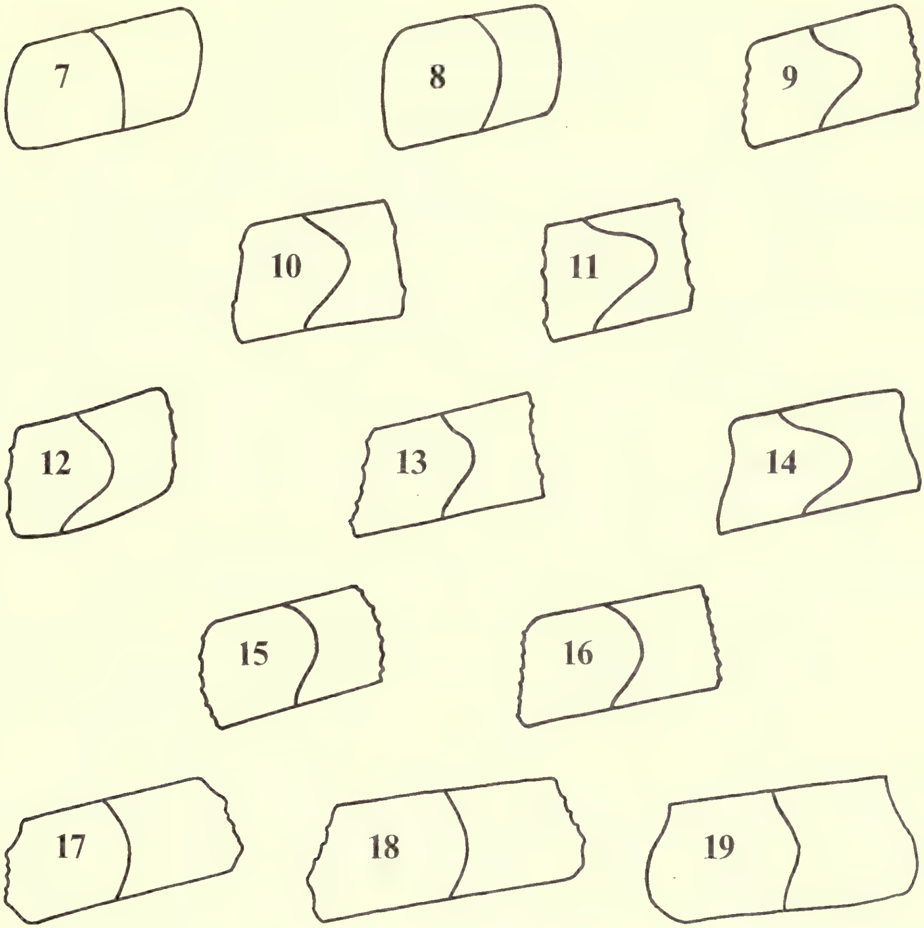
Measurements of the Holotype :

Height (as now preserved) . . .	75 mm.
Spire angle	13°
Height of penultimate whorl . . .	12 mm.
Diameter of penultimate whorl . .	19 mm.

DISCUSSION.—This species is included in the subgenus *Turritella* s. str. as its growth-lines have a simple, shallow sinus and a strong prosocline trend, as in the type-species of the genus. It differs from *T.* (*T.*) *unicarinata*, described below, in the presence of a greater number of spirals and of frequent collabral rugae.

OCCURRENCE. The holotype came from the Chalk Marl (Cenomanian) of Margett's Pit, Burham, Kent. The species has also been reported from the same formation at

Folkestone and from the Burwell Rock (Cenomanian) at Burwell and Reach, in Cambridgeshire.



Figs. 7–19. Diagrams of growth-lines of the species described in this paper.

7. *Turritella* (*Turritella*) *dibleyi* Newton.
8. *Turritella* (*Turritella*) *unicarinata* (S. Woodward).
9. *Turritella* (*Torquesia*) *granulata* J. de C. Sowerby.
10. *Turritella* (*Torquesia*) *tamra* sp. nov.
11. *Turritella* (*Torquesia*) *vibrayeana* d'Orbigny.
12. *Turritella* (*Torquesia*) *wagihi* sp. nov.
13. *Turritella* (*Torquesia*) *faizai* sp. nov.
14. *Turritella* (*Torquesia*) *hassani* sp. nov.
15. *Turritella ageri* sp. nov.
16. *Turritella sherborni* sp. nov.
17. *Mathilda coxi* sp. nov.
18. *Mathilda ahmadi* sp. nov.
19. " *Turritella* " *turbinata* J. de C. Sowerby.

Turritella (Turritella) unicarinata (S. Woodward)

(Pl. 28, figs. 3–5 ; Text-fig. 8)

1833. *Cerithium unicarinatum* S. Woodward, p. 49, pl. 6, fig. 21.
1854. *Nerinaea unicarinata* (Woodward) : Morris, p. 264.
1865. *Turritella unicarinata* (Woodward) : Tate, p. 37, pl. 3, fig. 7.

HOLOTYPE. Not traced.

DESCRIPTION. The shell is moderately large and slender. The earlier whorls, up to a diameter of 8 mm., are missing in the specimens studied. The whorls which are preserved are feebly and almost symmetrically convex in outline and the suture is moderately deep. The later whorls bear about 30 very finely beaded spiral threads, separated by equal interspaces nearly equal in width to the threads, but becoming slightly wider than them towards the anterior suture. Each interspace is usually occupied by one secondary spiral. The base is slightly convex and has an angular periphery. It is crossed by spirals of the same nature as those on the whorl-side. The growth-lines have a broad sinus without points of inflection and the growth-line chord is orthocline (Text-fig. 8). A furrow on the internal mould appears to be the impression of a depressed median spiral fold on the interior of the whorls. The aperture is subquadrate.

Measurements of a Typical Specimen (G.S.M. no. 28256) :

Height (as now preserved)	51 mm.
Spire angle	13°
Height of penultimate whorl	12 mm.
Diameter of penultimate whorl	16·5 mm.

DISCUSSION. This species has been referred to such different genera as *Cerithium*, *Nerinea* and *Turritella*. The absence of an anterior canal or notch excludes it from the first two genera and it also differs from *Nerinea* in the absence of internal folds (apart from the single one mentioned) and of a juxta-sutural sinus band. The entire aperture and other characters show that it belongs to *Turritella*, and it is included in *Turritella* s. str. on account of the simple arcuate form of its growth lines.

OCCURRENCE. The holotype was found in the Upper Chalk of Norwich, where internal moulds are frequent. The species also occurs in the Upper Chalk of Northern Ireland, where it is common in the White Limestone (Campanian) at Lisburn and rare in the Spongarian Zone (Santonian) at Woodburn.

Subgenus ***TORQUESIA*** Douvillé, 1929 : 55

TYPE SPECIES. *Turritella granulata* J. de C. Sowerby (designated by International Commission on Zoological Nomenclature, Opinion 493, 1957).

SUBGENERIC CHARACTERS. Shell medium-sized, more or less slender ; whorls flat to moderately convex, ornamented with beaded spiral cords ; growth-lines forming a rather deep sinus with its vertex nearly at mid-whorl and with points of inflection above and below it ; growth-line chord orthocline to feebly prosocline.

Turritella (Torquesia) granulata J. de C. Sowerby

(Pl. 30, figs. 10–14 ; Text-fig. 9)

1811. *Cerithium turritellatum* Parkinson, p. 71 (*non* Lamarck).
1816. *Turritella* sp. : Smith, p. 12, " Green Sand " pl., fig. 5.
1827. *Turritella granulata* J. de C. Sowerby, p. 125, pl. 565, fig. 1.
1840. *Turritella granulata* Sowerby : Geinitz, p. 44, pl. 15, figs. 7–11.
1842. *Turritella granulata* Sowerby : d'Orbigny, p. 46, pl. 153, figs. 5–7.
1843. *Turritella granulata* Sowerby : Geinitz, p. 10, pl. 1, fig. 18.
1845. *Turritella granulata* Sowerby : Geinitz, p. 325, pl. 14, figs. 9, 10.
1849. *Turritella granulata* Sowerby : Brown, p. 70, pl. 38, fig. 18.
1850. *Turritella granulatoides* d'Orbigny, p. 190.
1868. *Turritella granulata* Sowerby : Briart & Cornet, p. 29, pl. 3, figs. 43, 44.
1875. *Turritella granulata* Sowerby : Geinitz, p. 239, pl. 54, figs. 3, 4.
1920. *Turritella* (*Haustator*) *granulata* Sowerby : Roman & Mazeran, p. 44, pl. 5, fig. 21.
1920. *Turritella* (*Haustator*) *granulatoides* d'Orbigny : Roman & Mazeran, p. 44, pl. 5, figs. 17–20.

HOLOTYPE. In the British Museum (Natural History), reg. no. 43667.

DESCRIPTION. The shell is of medium size and moderately slender. The protoconch is not preserved in an uneroded state in the specimens studied. The whorl outline is feebly convex and the whorls are relatively high. The suture is at first superficial but becomes progressively more furrowed between the later whorls, which tend to become disjunct in some specimens. On the earliest whorls of which the ornament has been observed four beaded spiral cords are present in all variations of this species, and their interspaces soon become occupied by one or more spiral threads which are finely beaded. Some of these spiral threads increase in prominence during growth so that on the later whorls they become as strong as the primary cords, and, as a result, there may be as many as 7–8 principal spirals on the last whorl. The most posterior spiral cord is stronger than the others and is separated from them by a relatively broad spiral groove ; this feature is diagnostic of the species. On the later whorls, especially the last, the beads on the cords are located along conspicuous growth-lines, and those on the most posterior cord produce a feeble undulation of the suture. The base is convex and is ornamented with spiral cords crossed by growth-rugae. The aperture is oval, with a rounded anterior margin. The thin inner lip is reflected on the columella. The growth-lines have a deep U-shaped sinus and two points of inflection, one near each suture ; the growth-line chord is slightly prosocline (Text-fig. 9).

Measurements of Holotype :

Height	46 mm.
Spire angle	18°
Height of penultimate whorl . . .	8 mm.
Diameter of penultimate whorl . .	10 mm.

VARIABILITY. This species is rather variable. One variant is similar to the holotype except that its ornament consists even on the later whorls of only four principal cords with very conspicuous beads. It would appear that additional shelly matter was added during growth to the primary spirals instead of to secondary spirals in their interspaces. (See Pl. 30, fig. 14.)

DISCUSSION. The specimens figured by d'Orbigny (1842) as *T. granulata* had five spiral cords (not four, as stated by Roman & Mazeran, 1920), and subsequently d'Orbigny considered them to belong to a different species, *T. granulatoides*, distinguished from the true *T. granulata* by the smaller number of its spiral cords and by the deeper sinus of its growth-lines. The present writer has found that specimens agreeing with both forms occur in association at Blackdown, while Roman & Mazeran mention that they are found together in the Turonian of the Uchaux Basin (France). It thus seems reasonable to re-unite them as one species.

Cossmann (1912) referred *T. granulata* to Montfort's subgenus *Haustator* (type-species *Turritella imbricataria* Lamarck, Eocene). He included in this subgenus a great number of turritellids with growth-lines of the same type as those of the type-species, namely, with a deep sinus near the middle of the whorl and points of inflection above and below it. He admitted, however, that forms differing considerably from the type-species in whorl outline and ornament were thereby brought together. Roman & Mazeran (1920) also referred *T. granulata* to *Haustator*. Douvillé (1929), however, was of the opinion that Cossmann had interpreted *Haustator* too widely and considered that the group of Cretaceous species with rather similar growth-lines but commonly with a beaded cord near the posterior suture should constitute a new subgenus *Torquesia*. He cited as type-species of this new taxon " *T. granulosa* de Blackdown ", which the International Commission on Zoological Nomenclature, following a petition by Dr. J. Marwick, has decided was an unintentional error for *Turritella granulata*. Marwick (1957 : 160) rather doubts the taxonomic importance of beaded spiral cords, but nevertheless considers that *Torquesia* is a taxon in which many Cretaceous species may usefully be included. The growth-lines are more symmetrical and the upper point of inflection is more marked than in the type-species of *Haustator* as figured by Marwick (1957 : 146, text-fig. 14), and their general trend is less pronouncedly prosocline. *Torquesia* is, therefore, here accepted as a subgenus in which several English Cretaceous species can be included.

OCCURRENCE. *T. granulata* is very abundant in the Albian Greensand of its type-locality, Blackdown, Devon, although specimens retaining the initial whorls and showing the whole ornament clearly are very rare. Specimens from the Cenomanian of Warminster, Wilts., and of Devon (*falcatus* Zone) have also been examined. A queried record of the occurrence of the species in the Lower Greensand of Ingoldsthorpe, Norfolk (Forbes, 1845) is to be rejected.

T. granulata has been recorded from the Cenomanian of various parts of the European Continent, including the Elbe valley district of Saxony, where it occurs in both the Lower Quadersandstein and the Lower Pläner (Geinitz, 1874), Bohemia (Reuss, 1845), Bavaria (Söhle, 1896), the Baltic coastlands in glacial erratics (Noetling, 1885), and Belgium, where it occurs in the so-called *meule de Bracquegnies*. D'Orbigny (1842) and Roman & Mazeran (1920) have recorded it from the Turonian of Uchaux in France.

Turritella (Torquesia) tamra sp. nov.

(Pl. 28, fig. 1 ; Text-fig. 10)

HOLOTYPE. In the Sedgwick Museum (Cambridge), reg. no. B. 27329.

DESCRIPTION. The shell is small and slender. The actual protoconch is not preserved in the specimens studied and the earlier whorls are worn. The whorls are moderately high, with a slightly convex outline, and they are separated by a well-impressed suture. Four beaded primary cords are present when the whorl diameter is 2 mm. and on the later whorls the number of principal spirals has increased to about six, one of which is close to the anterior suture. These are separated by considerably wider interspaces occupied by from one to three spiral threads, some not very much weaker than the principal spirals. The beads on the spirals are weak and some are elongated in a spiral direction with the spaces between them varying in width. The base is convex and is bordered by the primary spiral which is seen just above the suture on the later spire whorls ; below this are three more primaries, decreasing in strength inwards, with fine secondary threads between them. The aperture is not preserved. The growth-lines have a deep sinus the vertex of which lies between the second and the third primary cord from the posterior suture, that is, well above the middle of the whorl ; there are two points of inflection. The growth-line chord is very slightly opisthocline (Text-fig. 10).

Measurements of the Holotype:

Height	26 mm.
Spire angle	14°
Height of penultimate whorl	3·5 mm.
Diameter of penultimate whorl . . .	5 mm.

DISCUSSION. Several other specimens of this species are preserved in the small piece of rock which contains the holotype, but only two (including one which has been registered separately as B. 27330) show any diagnostic characters.

This species is included in the subgenus *Torquesia* because of its growth-line pattern and of its ornament, which bears a general resemblance to that of *T. granulata*. It differs from that species, of which it is possibly the ancestor, in its smaller size, more convex whorl outline, weaker spirals, and fewer and weaker beads.

OCCURRENCE. Aptian, Lower Greensand, Atherfield Clay Series (bed known as the " Crackers "), Atherfield, Isle of Wight.

Turritella (Torquesia) vibrayeana d'Orbigny

(Pl. 31, figs. 17–22 ; Text-fig. 11)

1842. *Turritella vibrayeana* d'Orbigny, p. 37, pl. 151, figs. 10–12.
1860. *Turritella vibrayeana* d'Orbigny : Mackie, p. 324, fig. 34.
1862. *Turritella vibrayeana* d'Orbigny : Pictet & Campiche, p. 315, pl. 72, figs. 5–7.
1896. *Turritella vibrayeana* d'Orbigny : Cossmann, p. 255, pl. 1, figs. 24–26.
1903. *Turritella vibrayeana* d'Orbigny : Doncieux, p. 301, pl. 1, fig. 1.
1954. *Turritella* cf. *vibrayeana* d'Orbigny : Gortani, p. 75, pl. 16, figs. 2*a*, *b*.

SYNTYPES. Nine specimens in the d'Orbigny Collection in the Muséum National d'Histoire Naturelle, Paris, reg. no. 5847.

DESCRIPTION. The shell is of small to medium size and very slender, with relatively high whorls. The whorl sides are usually flat but may be feebly convex; the suture is superficial or slightly furrowed. The initial whorls have a tricostate ornament. The three primary spiral cords may persist on the later whorls without the addition of other strong spirals (Pl. 31, fig. 19), but usually a fourth principal cord is added near the posterior suture (Pl. 31, fig. 20), while a fifth may appear in the most posterior interspace (Pl. 31, fig. 18) and a sixth in the most anterior interspace (Pl. 31, fig. 22). The spiral cords are beaded, some rather coarsely, others faintly. Some of the interspaces are almost equal to the primary cords in width, but most of them are wider, sometimes as much as five to six times as wide (Pl. 31, fig. 17). Secondary threads, variable in number, occupy these interspaces, and usually one or two are more prominent than the rest. The base is slightly convex, with spiral cords and threads crossed by growth-lines. The aperture is oval and evenly rounded anteriorly. The growth-lines are of about the same strength as the secondary spiral threads. They show a deep sinus with its vertex near the middle of the whorl and two points of inflection, one near each suture. The growth-line chord is almost orthocline (Text-fig. 11).

Measurements of a Typical Specimen (B.M., no. G.73791):

Height	40 mm.
Spire angle	10°
Height of penultimate whorl	3·5 mm.
Diameter of penultimate whorl	6 mm.

DISCUSSION. *Turritella vibrayeana* has been described by previous authors as having four primary beaded spiral cords alternating with secondary ones. Actually, it is a highly variable species. At one extreme of the range of variation are forms retaining on the later whorls the same number of primary spiral cords as are found on the initial ones, and at the other extreme are specimens in which as many as three additional principal cords have been added. There appears to be no justification for separating shells with additional spiral cords on the later whorls as distinct species or subspecies, since all specimens show the same growth-line pattern and the ornament of the initial whorls is always tricostate. The variation in the number of principal cords may be due to unimportant environmental or physiological factors, although its causes may be merely genetic.

The first reference in the literature to specimens belonging to this species was when Michelin (1838 : 99) referred a *Turritella* from the Gault of the Aube Department of France to *Turritella rigida* J. de C. Sowerby (1833, pl. 38, fig. 19), a species from Gosau, in Austria. *T. rigida* has a prominent posterior tuberculate spiral cord on which the tubercles are markedly elongated and extend to the suture, and this feature is not found in specimens from the Gault. In view of these differences d'Orbigny (1842) erected his new species *T. vibrayeana* for the latter. The figures of Pictet & Campiche, illustrating specimens from Switzerland, agree with our description.

Doncieux (1903), when recording specimens from the Gault of the eastern Corbières, in the south of France, stated that they differed from the holotype of d'Orbigny in the inequality of the spiral cords (the most anterior of these being the strongest) and also of the secondary spirals. His figures, however, do not show these features. Cossmann (1912) included *T. vibrayeana* in the subgenus *Haustator*. The present writer agrees that relationship with *Turritella granulata* is indicated by the growth-line pattern and by the general character of the ornament. *T. vibrayeana* is, therefore, now included in the subgenus *Torquesia*. Merriam (1941), in discussing his "first stock" of *T. tolenasensis* Merriam, referred to *T. vibrayeana* as showing similarities to some American species.

Occurrence. All the specimens examined in the preparation of this paper are from the Gault of Folkestone, Kent, except one (G.49825) which was collected by Dr. W. D. Lang from the Lower Gault of Fairy Dell, Stonebarrow, Charmouth, Dorset. *T. vibrayeana* has been found in the Albian of France at several localities in the Aube Department and the eastern Corbières, and it has also been recorded from Switzerland, Italy and Russia.

Turritella (Torquesia) wagihi, sp. nov.

(Pl. 29, fig. 6; Text-fig. 12)

Holotype. In the Geological Survey Museum, reg. no. 93745.

Description. The shell is of medium size and moderately slender. The whorls are feebly convex, with a weak carina close to the anterior suture, giving them a subimbricate appearance. The protoconch is not preserved. The earliest whorls seen are tricostate, with primary cords lying at the anterior quarter, the middle, and the posterior quarter respectively. The number of principal spiral cords remains the same on the later whorls, but they have moved a little further forward so that the space behind the most posterior cord is greater than that in front of the most anterior one. These spirals show a marked difference in strength and in the number of beads on them. Thus, while the beads are relatively strong and wide apart on the most posterior cord, those on the most anterior one are more numerous, closer, and weaker. The primary interspaces are three to four times as wide as the primary spiral cords, and each is occupied by two secondary spiral cords and four or five spiral threads. The aperture and base are not preserved in the holotype. The growth-lines have a broad and rather shallow sinus with its vertex at about the middle of the whorl and two points of inflection; the growth-line chord is slightly opisthocline (Text-fig. 12).

Measurements of the Holotype:

Height	49 mm.
Spire angle	14°
Height of penultimate whorl . . .	5 mm.
Diameter of penultimate whorl . .	10 mm.

Discussion. The holotype, the only specimen seen, is crushed and its spire angle may be greater than was originally the case. This species bears some resemblance to *Turritella vibrayeana* and its variations, but can be distinguished by the shape of the shell, the lower whorls, the more convex whorl outline, the peculiar difference in the granulation of the primary spiral cords and the development of the spiral ornament during the ontogeny of the shell. It differs from *T. marticensis* Matheron (1843 : 240, pl. 39, fig. 16) in the presence of the anterior carination and in the nature of the ornament. The growth-lines are not indicated clearly enough in Matheron's figure to allow comparison to be made with those of the present species.

OCCURRENCE. Albian, Gault, Folkestone, Kent.

Turritella (Torquesia) faizai sp. nov.

(Pl. 30, fig. 15 ; Text-fig. 13)

HOLOTYPE. In the Sedgwick Museum (Cambridge), reg. no. B.44621.

DESCRIPTION. The shell is of medium size and moderately slender. The earlier whorls have a slightly convex outline with a feeble anterior carination, but the later whorls become concave mesially, with anterior and posterior convexities. The suture is moderately deep. The protoconch is broken off in the holotype. The earliest preserved whorls are tricostate, the most anterior spiral cord coinciding with the carination. On later whorls a secondary spiral cord is developed behind each primary spiral, and these secondaries increase in strength rapidly until they become as strong as the primaries, so that the total number of principal spiral cords is increased to six. The cords are finely beaded and are separated by wider interspaces most of which are occupied by one secondary and two tertiary threads. The most anterior primary cord is separated from the adjacent suture by an interspace wider than that between the posterior primary and the corresponding suture. A secondary spiral which develops in this latter interspace becomes as strong as the most posterior primary on the later whorls and fuses with it to form a strong astragal[1] which affects the whorl outline. The base is almost flat, with a rounded edge, and bears concentric cords which alternate in strength. The aperture is broken away but was evidently subquadrangular. The growth-lines have a deep, broad sinus and points of inflection coinciding with the anterior and posterior convexities. The growth-line chord is almost orthocline (Text-fig. 13).

Measurements of the Holotype :

Height	53 mm.
Spire angle	16°
Height of penultimate whorl . . .	8 mm.
Diameter of penultimate whorl . .	15 mm.

DISCUSSION. This species is distinguished from *Turritella* (*Torquesia*) ***hassani***, described below, by the relative weakness of the astragal on the posterior part of the whorls and by the anterior convexity of the whorls. It also has fewer secondary threads between the principal spiral cords.

OCCURRENCE. Albian of Devon ; the holotype came from the Greensand of Blackdown and specimens have also been found in the Upper Greensand of Peak Hill (west of Sidmouth), Seaton and Beer.

---

[1] Astragal.—A moderately broad, parallel-sided elevation with a rounded profile (architectural term).

Turritella (Torquesia) hassani sp. nov.

(Pl. 28, fig. 2; Pl. 29, fig. 9; Text-fig. 14)

HOLOTYPE. In the British Museum (Natural History), reg. no. G.49907.

DESCRIPTION. The shell, not known complete, is of medium size, slender, and nerineiform. The whorl outline is flat or slightly concave and the sutures are superficial. A rounded posterior astragal, occupying about one-fifth of the height of the whorl, is developed just below the suture. Eight or nine very faintly beaded primary spiral cords are distributed equally over the anterior four-fifths of the whorl; the interspaces are two to three times as wide as the cords. These interspaces are occupied by four to seven fine spiral threads of which the middle one is sometimes stronger than the others; similar spiral threads cover the rounded posterior astragal. The base and aperture are not preserved in the available specimens. The growth-lines have a deep sinus with its vertex at the middle of the whorl and two points of inflection. The growth-line chord is slightly prosocline (Text-fig. 14).

Measurements of the Holotype :

Height (four mid-spire whorls) . . .	40·5 mm.
Spire angle	12½°
Height of last preserved whorl . . .	9 mm.
Diameter of last preserved whorl . . .	14 mm.

DISCUSSION. This species is founded on three imperfect specimens now in the British Museum (Natural History), two collected by Mr. T. F. Grimsdale, the third by Mr. C. W. Wright. It differs from the other turritellids described in this work in having concave whorls with a rounded posterior astragal crossed by spiral threads and in other details of ornament. The growth-line pattern is similar to that of *Turritella* (*Torquesia*) *granulata* J. de C. Sowerby, and this permits its inclusion in the same subgenus as that species.

OCCURRENCE. Cenomanian Limestone (Bed B of Jukes-Browne), " near Seaton, Devon " (type-locality). Same bed, between Havencliff and Dowlands, east of Seaton, Devon (*ex* C. W. Wright Collection).

Subgenus novum ?

In the two species described next the growth-lines have a broad sinus with its vertex at about mid-whorl and an inflection point close to the lower suture; the growth-line chord is almost orthocline. The whorls are feebly convex and the ornament is of beaded spiral cords. Of the turritellid growth-lines figured by Marwick (1957 : 146), those of *Pareora* (fig. 25) are most like those of the two new species, but the sinus is deeper and its vertex is higher on the whorl. In *Sigmesalia* (Marwick's fig. 31) the growth-lines rather resemble those of these species, but the point of inflection coincides with the lower suture. In other characters there is little resemblance between the forms now described and either *Pareora* or *Sigmesalia*. It is probable that they belong to a new subgenus, but since neither their apertures nor their initial whorls can be studied this could not at present be defined satisfactorily.

Turritella ageri sp. nov.

(Pl. 32, fig. 25; Text-fig. 15)

Holotype. In the British Museum (Natural History), reg. no. G.74106.

Description. The shell is moderately slender and of medium size. The whorl outline is feebly and symmetrically convex, the suture very slightly impressed. The initial whorls, up to a diameter of 3 mm., are not preserved in the specimens studied. The whorls now preserved have 6–8 coarsely beaded spiral cords which increase in strength during growth. On the last whorl the width of the interspaces is equal to or slightly exceeds that of the cords. Each interspace is occupied by three or four spiral threads, the middle one of which may be more prominent than the others and ultimately become as strong as the primary cords. The beads are coarse, more or less rounded, and closely spaced. The base is slightly convex, with a rounded periphery, and is crossed by a number of spiral threads alternating in strength. The aperture is not complete in the holotype, but it can be inferred from the outline of the last whorl that it was more or less elliptical. The inner lip is reflected over the short and thick columella. The growth-lines have a broad, moderately deep sinus, the vertex of which lies on the third spiral cord from the posterior suture, that is, at about the posterior two-fifths of the height of the whorl. They straighten out to a point of inflection on the most anterior spiral cord. The growth-line chord is almost orthocline (Text-fig. 15).

Measurements of the Holotype:

Height	47 mm.
Spire angle	16°
Height of penultimate whorl . . .	8 mm.
Diameter of penultimate whorl . .	14 mm.

Discussion. This new species can be easily distinguished from similar forms, such as *Turritella* (*Torquesia*) *granulata* J. de C. Sowerby, by the absence of a very strong posterior spiral cord, by the prominence of the spirals on the last whorl, by its very coarse and rounded beads, and by the growth-line pattern.

Occurrence. Albian, Greensand, Blackdown, Devon.

Turritella sherborni sp. nov.

(Pl. 30, fig. 16; Text-fig. 16)

Holotype. In the British Museum (Natural History), reg. no. G.74107.

Description. The shell is of medium size, with whorls which are subimbricate owing to the presence of a weak carina which coincides with the second spiral cord from the anterior suture; above this carina the whorl surface is almost flat. The sutures are slightly impressed. The initial whorls, up to a diameter of 4 mm., are not preserved in the holotype. On the whorls which are still seen there are seven equal spiral cords ornamented with small, spirally elongated beads separated by constrictions which are nearly equal in width to the beads. The interspaces between the spiral cords are nearly double the width of the latter and are occupied by spiral threads, one or two of which may be stronger than the rest. The spiral threads show faint constrictions corresponding to those of the primary spiral cords. The base is rather obscured by adherent matrix in the holotype, but has a rounded periphery below which its surface is slightly convex. The aperture has an evenly rounded anterior margin and its height is about equal to its width. The growth-lines have a broad and moderately deep sinus the vertex of which lies just above the middle of the height of the whorl. They straighten out to a point of inflection just above the lower suture. The growth-line chord is almost orthocline (Text-fig. 16).

Measurements of the Holotype:

Height	30 mm.
Spire angle	16°
Height of penultimate whorl . . .	6 mm.
Diameter of penultimate whorl . .	10 mm.

Discussion. This new species much resembles *Turritella* (*Torquesia*) *granulata* J. de C. Sowerby, but differs in the equality of its spiral cords, in the presence of the anterior carination, and in the nature of the growth-lines. It shows a great similarity to *T. cenomanensis* d'Orbigny, as figured by Guéranger (1867, pl. 9, figs. 10, 11), but differs in having anteriorly carinate whorls, and probably also in the nature of the spiral cords, which are not clearly shown in Guéranger's figures. D'Orbigny (1850, p. 148) referred *T. granulata* Geinitz (1840, pl. 15, figs. 7–11, *non* Sowerby) to *T. cenomanensis*, but Geinitz (1874 : 161) later included pl. 15, fig. 9 in the synonymy of *T. multistriata* Reuss. *T. cenomanensis* was included by Cossmann in the subgenus *Haustator*, but its growth-lines are unlike those of the type-species of that subgenus.

The new species *T. sherborni* differs from *T. ageri*, described above, in its anterior carination and finer granulation.

Occurrence. Albian, Greensand, Blackdown, Devon.

Family Mathildidae Cossmann, 1912

Genus ***MATHILDA*** Semper, 1865 : 330

Type species. *Turbo quadricarinatus* Brocchi, 1814 (by subsequent designation, de Boury, 1883).

Mathilda coxi sp. nov.

(Pl. 32, fig. 23 ; Text-fig. 17)

Holotype. In the Sedgwick Museum (Cambridge), reg. no. B.27336.

Description. The shell is of small-medium size and broadly turriculate. Details of the protoconch have been a little obscured by erosion. Although not conspicuously heterostrophic, it exhibits a distinct discontinuity of coiling; its first complete whorl is an open one with a gap in the middle, and the actual nucleus seems to be partly obscured by this whorl. The first two visible whorls are smooth and rounded in outline, while the third develops a median carina. On the next succeeding whorls a second carina makes its appearance just in front of the posterior suture, but the original carina remains the more prominent. The concavity between these carinae, which come respectively to occupy positions at about the lower third and slightly above the upper third of the whorl, is reduced on the later whorls, which are biangular with an almost flat outer face. The suture is deep. The outer face of the later whorls is occupied by two to three spiral cords of primary strength, separated by interspaces which are of the same width or slightly narrower. Each interspace is occupied by one or by two secondary spirals. The area between each carina and the adjacent suture is similarly ornamented, but the spirals on the anterior area are the most prominent. On the last whorl two additional spiral cords of primary strength and below them a third carina become visible just above the suture. The periphery of the convex base is formed by a spiral keel continuing this third carina; below it is a further carina, and the remainder of the base bears concentric threads of two orders of strength. Where uneroded, the whole surface of the shell bears a delicate ornament of closely and regularly spaced collabral threads. The aperture is oval, with the inner lip slightly reflected. The growth-lines between the sutures form a broad arch, the chord of which is almost orthocline (Text-fig. 17).

Measurements of the Holotype:

Height	21 mm.
Spire angle	30°
Height of penultimate whorl . . .	5 mm.
Diameter of penultimate whorl . .	10 mm.

DISCUSSION. The protoconch of the holotype of this species is not so obviously heterostrophic as in some of the figures of Tertiary species of *Mathilda* published by Semper (1865) and de Boury (1883), showing specimens in which the axis of coiling of the initial whorls is at right angles to that of the shell axis. In a specimen from the Miocene of southern France in the Wrigley Collection in the British Museum (Natural History), identified as belonging to the var. *semperi* Tournouer of the type-species of the genus, *M. quadricarinata* (Brocchi), the protoconch is, however, very similar to that of the species now described, and in some of the Paris Basin Eocene shells figured by de Boury (1883, pl. 5, figs. 7*a*, 9*a*, 10*a*, 11*a*) it also seems to be of a comparable type. In its general form and ornament as well as in its broadly arched growth-lines the present shell seems to be a typical *Mathilda*.

Cossmann (1912 : 10) recognizes two Cretaceous representatives of the genus, *M. douvillei* Cossmann (1912, pl. 1, figs. 3–5) and *M. faucignyana* (Pictet & Roux) (1849 : 166, pl. 16, fig. 1, *sub Turritella*), both Albian in age. *M. douvillei* is of about the same size and proportions as the new species *M. coxi*, but its ornament, although of the same general character, differs in detail.

Occurrence. Aptian, Lower Greensand, Atherfield Clay Series (bed known as the " Crackers "), near Atherfield, Isle of Wight.

Mathilda ahmadi sp. nov.

(Pl. 32, fig. 24 ; Text-fig. 18)

Holotype. In the Sedgwick Museum (Cambridge), reg. no. B.44649.

Description. The shell is of small-medium size, turriculate, and moderately broad-spired. The protoconch is missing in the specimens studied, the earliest preserved whorl being about 1·5 mm. in diameter. All the whorls now present are bicarinate anteriorly, the posterior carina being slightly the more prominent and placed well below their median line. The interspace between the carinae is narrower than the latter and is occupied on the later whorls by one or two secondary spirals. The part of the whorl posterior to the carinae is occupied by two to five primary spirals which decrease in strength posteriorly and are separated by interspaces the width of which is about the same as that of the spirals or slightly greater ; each interspace is occupied by one secondary spiral. On the later whorls the more posterior of the main carinae carries spiral threads or (in one specimen) splits up into two cords. The narrow area anterior to the carinae is occupied by two or more secondary spirals, and a further carina becomes visible on the last whorl, continuing the line of the suture. Everywhere very fine and numerous, regularly spaced collabral threads form a cancellate ornament with the spirals. The base is convex and the spiral cord which forms its periphery is succeeded inwards by a number of weaker spirals, alternating in strength. The aperture is rounded and the inner lip thin and reflected. The growth-lines form a broad, shallow arch with its vertex at about the middle of the whorl ; the growth-line chord is almost orthocline (Text-fig. 18).

Measurements of the Holotype :

Height	22 mm.
Spire angle	18°
Height of penultimate whorl . . .	4 mm.
Diameter of penultimate whorl . .	8 mm.

Discussion. This species bears a general resemblance to *Mathilda coxi*, but differs in the more anterior position of its carinae and the narrower space separating them, as well as in other details of ornament.

Occurrence. Albian, Greensand, Blackdown, Devon.

INCERTAE SEDIS

" Turritella " turbinata J. de C. Sowerby

(Pl. 32, figs. 26, 27 ; Text-fig. 19)

1850. *Turritella turbinata* J. de C. Sowerby, *in* Dixon, p. 349, pl. 29, fig. 2.

Holotype. In the British Museum (Natural History), reg. no. 44520.

Description. The shell is large and phasianelliform. The earlier whorls, up to a diameter of about 15 mm., are not preserved in the specimens studied. The outline of the later whorls is strongly convex except for a slight concavity near the posterior suture, the diameter of those forming the spire being almost three times their height. The whorls are ornamented with about 40 spiral threads which are finely serrated and separated by interspaces equal to or narrower than their own width. The threads are of equal strength except for the most posterior six to eight, which are more prominent than the rest. The base is convex, with a rounded periphery, and is crossed by spiral threads similar to those on the outer face of the whorls. The apertural margin is not preserved intact in the available specimens, but, so far as can be seen, it was evenly rounded anteriorly. The growth-lines have a broad, shallow sinus, and a point of inflection near each suture ; the growth-line chord is almost orthocline (Text-fig. 19).

Measurements of Largest Specimen Examined (B.M., no. 98208) :

Height (allowing for missing apex)	*c.*115 mm.
Spire angle	34°
Height of penultimate whorl	23 mm.
Diameter of penultimate whorl	52 mm.

DISCUSSION. In the holotype the last whorl has been distorted by pressure in a direction parallel to the axis of the shell, with the result that its height has been reduced and the convexity of its outline increased. The specimen of which the measurements are quoted above seems to be undistorted, but the convexity of the later part of the last whorl at the periphery is stronger than that of the spire whorls.

This species appears to belong to a new genus which probably should be excluded from the Turritellidae. Until more perfect specimens are available, however, no adequate definition of this genus could be given. In its large size and *Phasianella*-like shape *T. turbinata* recalls the long-ranging Jurassic species *Bourguetia saemanni* (Oppel) (*B. striata* (J. Sowerby)), in which, however, the growth-lines are scarcely arched and slightly opisthocline and the last whorl and aperture are proportionately higher. *Bourguetia* is referred to the family Pseudomelaniidae, from which, however, the growth-lines would appear to exclude *T. turbinata*.

OCCURRENCE. Cenomanian, Chalk Marl, Sussex (holotype). Same formation, Ventnor, Isle of Wight.

REFERENCES

BOURY, E. DE. 1883. Description d'espèces nouvelles de *Mathilda* du Bassin de Paris, et révision du genre. *J. Conchyliol.*, Paris, **31** : 110–153, pl. 5.

BRIART, A. & CORNET, F. L. 1868. Description minéralogique, géologique et paléontologique de la Meule de Bracquegnies. *Mém. Sav. étr. Acad. R. Belg.*, Bruxelles, **34** : 1–92, pls. 1–8.

BROCCHI, G. 1814. *Conchiologia fossile subappenina con osservazioni geologiche.* 712 pp., 16 pls. Milano.

BROWN, T. 1849. *Fossil conchology of Great Britain and Ireland.* viii + 275 pp., pls. 1–98. London.

COSSMANN, M. 1896. Observations sur quelques coquilles crétaciques recueillies en France. *C. R. Ass. franç. Av. Sci. (Carthage)*, **25** (2) : 243–269, pls. 1, 2.

—— 1906. *Essais de paléoconchologie comparée*, **7**. 261 pp., 14 pls. Paris.

—— 1912. *Essais de paléoconchologie comparée*, **9**. 215 pp., 10 pls. Paris.

—— 1916. *Essais de paléoconchologie comparée*, **10**. 292 pp., 12 pls. Paris.

DIXON, F. 1850. *The geology and fossils of the Tertiary and Cretaceous formations of Sussex.* xvi + 423 + xvi pp., 40 pls. London.

DOLLFUS, G. F. 1926. Critique de la classification des Turritelles. *Bull. Soc. géol. Fr.*, Paris (4), **26** : 27–32.

DONCIEUX, L. 1903. Monographie géologique et paléontologique des Corbières orientales. *Ann. Univ. Lyon*, (N.S.) **1**, 11. 377 pp., 7 pls., 1 map.

DOUVILLÉ, H. 1929. Les couches à *Cardita Beaumonti* dans le Sind. *Palaeont. indica* (N.S.) **10**, mem. 3, fasc. 2 : 27–73, pls. 5–11.

FORBES, E. 1845. Catalogue of Lower Greensand fossils in the Museum of the Geological Society. *Quart. J. geol. Soc. Lond.*, **1** : 237–250, 345–355.

GEINITZ, H. B. 1839–42. *Characteristik der Schichten und Petrefacten des sächsisch-böhmischen Kreidegebirges.* 116 + xxv pp., 24 pls. Dresden & Leipzig.

—— 1843. *Die Versteineringen von Kieslingswalda und Nachtrag zur Characteristik des sächsisch-böhmischen Kreidegebirges.* ix + 23 pp., 6 pls. Dresden & Leipzig.

—— 1845–46. *Grundriss der Versteinerungskunde.* 815 pp., 26 pls. Dresden & Leipzig.

—— 1874. Das Elbthalgebirge in Sächsen. Abteil 1, Der Untere Quader ; Teil VII, Gasteropoden. *Palaeontographica*, Stuttgart, **20**, 1 : 239–276, pls. 53–60. Abteil 2, Der Mittlere und Obere Quader ; Teil V, Gasteropoden und Cephalopoden. *Palaeontographica*, Stuttgart, **20**, 2 : 161–198, pls. 29–46.

GORTANI, M. 1954. *La fauna mesocretacea degli strati di Grana.* 101 pp., 16 pls. Roma (Accad. naz. Lincei).

GUÉRANGER, M. E. 1867. *Album paléontologique du Départment de la Sarthe représentant au moyen de la photographie les fossiles receueillis dans cette circonscription.* 20 pp., 25 pls. Le Mans.

GUILLAUME, L. 1924. Essai sur la classification des Turritelles, ainsi que sur leur évolution et leurs migrations, depuis le début des temps tertiaires. *Bull. Soc. géol. Fr.*, Paris (4) **24** : 281–311, pls. 10, 11.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE. 1957. Opinion 493. Designation under the Plenary Powers of a type species in harmony with established usage for the genus *Torquesia* Douvillé, 1929 (Class Gastropoda). *Opinions and Declarations rendered*, **17** : 255–264.

LAMARCK, J. 1799. Prodrome d'une nouvelle classification des coquilles. *Mém. Soc. Hist. nat. Paris* (1) **1** : 63–91.

MACKIE, S. J. 1860. Geological localities. 1, Folkestone. *The Geologist*, **3** : 41–45, 81–90, 121–131, 201–207, 281–284, 321–327, 353–357, 393–396.

MARWICK, J. 1957. Generic revision of the Turritellidae. *Proc. malac. Soc. London*, **32** : 144–166.

MATHERON, P. 1842–3. *Catalogue méthodique et descriptif des corps organisés fossiles du Département des Bouches du Rhône et lieux circonvoisins.* 269 pp., 41 pls. Marseille.

MERRIAM, C. W. 1941. Fossil Turritellas from the Pacific coast region of North America. *Univ. Cal. Bull. geol. Sci.*, **26**, 1. v + 129 pp., 41 pls., map.

MICHELIN, H. 1838. Note sur une argile dépendant du Gault observée au Gaty, commune de Gérodot, Département de l'Aube. *Mém. Soc. géol. Fr.*, Paris, **3** : 97–103, pl. 12.

MONTFORT, P. D. DE. 1810. *Conchyliologie systématique et classification méthodique de coquilles*, **2**. 676 pp., Paris.

MORRIS, J. 1854. *A catalogue of British fossils*, 2nd edit. vii + 372 pp. London.

NEWTON, R. B. 1918. Notes on a new species of *Turritella* and a naticoid shell referred to the genus *Gyrodes* from British Cretaceous rocks. *Proc. geol. Ass.*, Lond., **29** : 97–105, pl. 10.

NOETLING, F. 1885. Die Fauna der baltischen Cenoman-geschiebe. *Geol. paläont. Abh.*, Berlin, **2** : 199–247 ; pl. 16–23.

ORBIGNY, A. D'. 1842. *Paléontologie française, terrains crétacés. 2. Gasteropodes.* 456 pp., pls. 149–236. Paris.

—— 1850. *Prodrome de paléontologie stratigraphique universelle des animaux mollusques et rayonnés*, **2**. 428 pp. Paris.

PARKINSON, J. 1811. *Organic remains of a former world*, **3**. iv + 479 pp., 22 pls. London.

PICTET, F. J. & CAMPICHE, G. 1861–64. Description des fossiles du terrain cretacé des environs de Sainte-Croix. *Matériaux pour la Paléontologie suisse*, **3** : 752 pp., pls. 44–98. Genève.

PICTET, F. J. & ROUX, W. 1849. *Description des mollusques fossiles qui se trouvent dans les grès verts des environs de Genève.* 558 pp., 51 pls. Genève.

REUSS, A. E. 1845. *Die Versteinerungen der böhmischen Kreideformation.* Pt. 1, iv + 58 pp., 13 pls. ; Pt. 2, iv + 148 pp., pls. 14–51. Stuttgart.

ROMAN, F. & MAZERAN, P. 1920. Monographie paléontologique de la faune turonien du Bassin d'Uchaux et de ses dépendences. *Arch. Mus. Hist. nat.*, Lyon, **12**, Mém. 2. 137 pp., 11 pls.

SEMPER, O. 1865. Du genre *Mathilda*. Additions à la monographie du genre *Mathilda*. *J. Conchyliol.*, Paris, **13** : 328–345, pl. 13.

SMITH, W. 1816–19. *Strata identified by organized fossils.* 32 pp., 18 pls. London. (Pp. 1–16, pls. 1–8, 1816 ; pp. 17–24, pls. 9–13, 1817 ; pp. 25–32, pls. 14–18, 1819.)

SÖHLE, U. 1896. Geologische Aufnahme des Labergebirges bei Oberammergau mit besonderer Berücksichtigung des Cenomans in den bayerischen Alpen. *Geogn. Jh.*, Cassel, **9** : 1–66, pls. 1–8.

SOWERBY, J. DE C. 1827. *The mineral conchology of Great Britain*, **6**. 235 pp., pls. 504–609. London.

—— 1833. *In* SEDGWICK, A. & MURCHISON, R. I. A sketch of the structure of the Eastern Alps with sections through the newer formations on the Northern flanks of the chain and through the Tertiary deposits of Styria. *Trans. geol. Soc. Lond.* (2) **3** : 310–420, pls. 35–40.

TATE, R. 1865. On the correlation of the Cretaceous formations of the N.E. of Ireland. *Quart. J. geol. Soc. Lond.*, **21** : 15–44, pls. 3–5.

WOODWARD, S. P. 1833. *Outline of the geology of Norfolk.* 54 pp., 6 pls., 5 maps. Norwich.

EXPLANATION OF PLATES

Specimens with numbers prefixed by BM, GSM, or SM are preserved in the British Museum (Natural History), London, the Geological Survey and Museum, London, and the Sedgwick Museum, Cambridge, respectively. Where specimens are preserved on a block of matrix, the vertical line indicates the length of the actual shell.

PLATE 28

FIG. 1. *Turritella* (*Torquesia*) ***tamra*** sp. nov. Aptian, Lower Greensand, Atherfield Clay Series (bed known as the "Crackers"), near Atherfield, Isle of Wight. Holotype (bottom right-hand specimen) and paratypes. SM, B. 27329–30. × 2 . p. 185

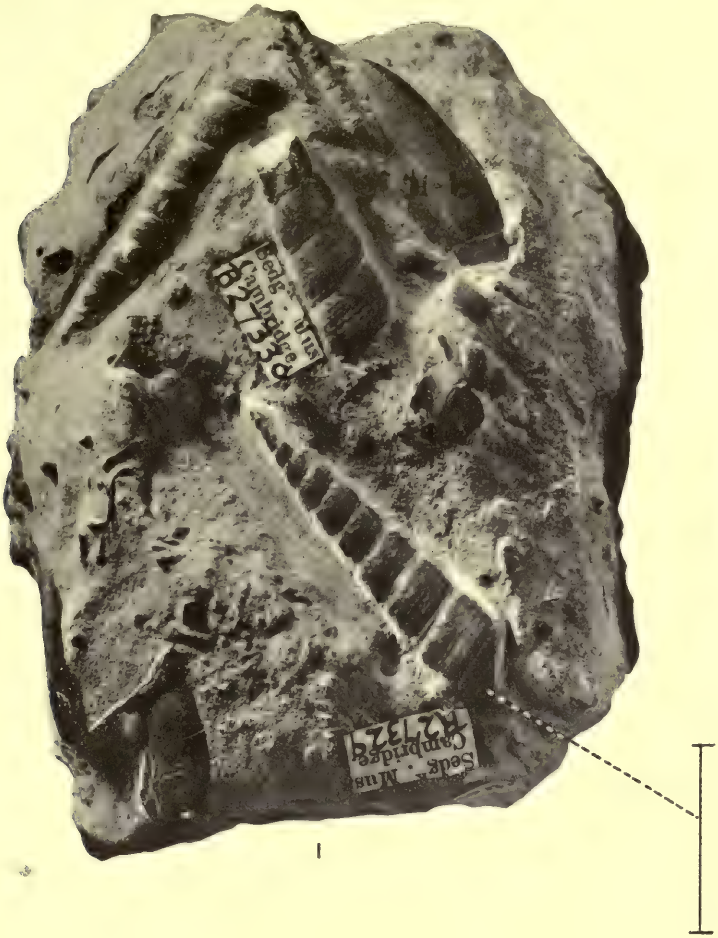
FIG. 2. *Turritella* (*Torquesia*) ***hassani*** sp. nov. Cenomanian Limestone (bed B of Jukes-Browne), "near Seaton, Devon". Holotype. BM, G. 49907. × 2. (See also Pl. 29, fig. 9.) . . . . p. 189

FIG. 3. *Turritella* (*Turritella*) *unicarinata* (S. Woodward). Upper Chalk, Lisburn, Co. Antrim, Ireland. GSM, 93759. × 2. . . . . p. 182

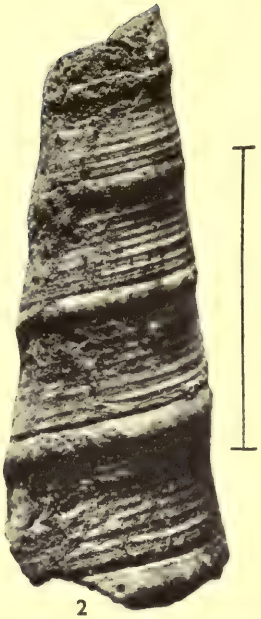
FIG. 4. Same species, basal view. Same locality. GSM, 93755. × 2.

FIG. 5. Same species. Upper Chalk, White limestone, Northern Ireland. GSM, 28256. × 1½.

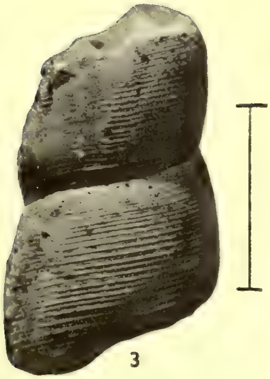
BRITISH MUSEUM


Sedg. Mus
Cambridge
B27338
Sedg. Mus
Cambridge
B27324

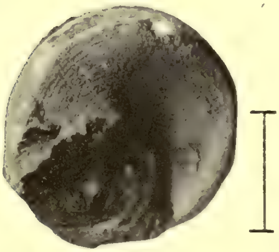
1



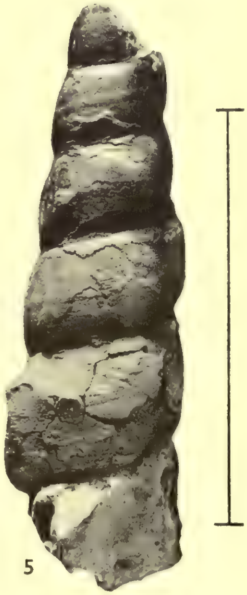
2



3



4



5

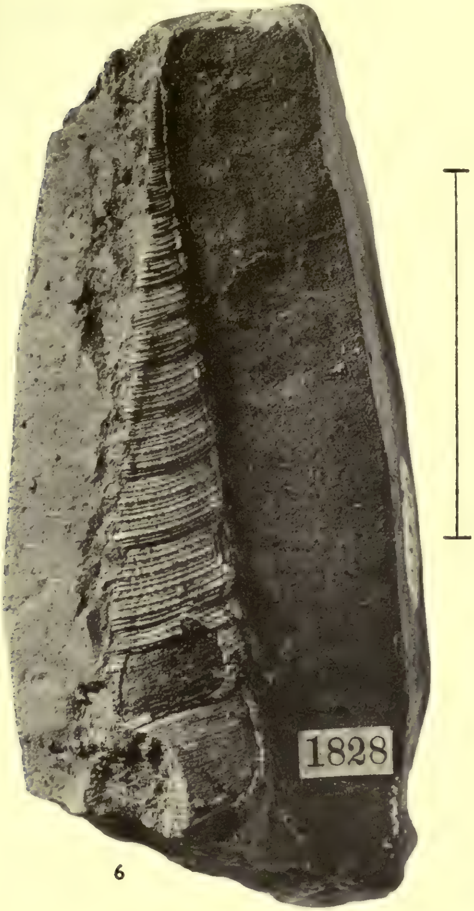
TURRITELLA s.str., TURRITELLA (TORQUESIA)

PLATE 29

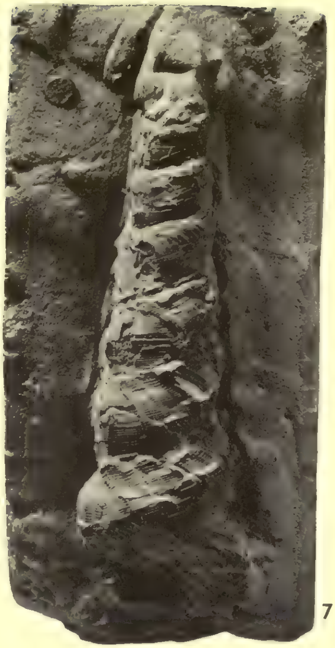
FIG. 6. *Turritella* (*Torquesia*) ***wagihi*** sp. nov. Albian, Gault, Folkestone, Kent. Holotype. GSM, 93745. ×2 . . . . p. 187

FIGS. 7, 8. *Turritella* (*Turritella*) *dibleyi* Newton. Chalk Marl (Cenomanian), Margett's Pit, Burham, Kent. Holotype. BM, G. 29362. ×1 (fig. 7); detail, showing ornament, ×3 (fig. 8) . . . . p. 180

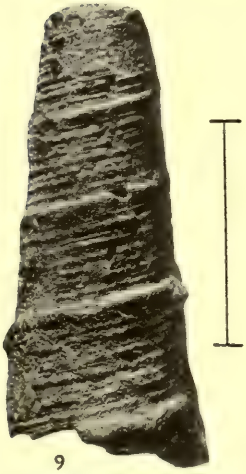
FIG. 9. *Turritella* (*Torquesia*) ***hassani*** sp. nov. Cenomanian Limestone (bed B of Jukes-Browne), " near Seaton, Devon ". Paratype. BM, GG. 2320. ×2. (See also Pl. 28, fig. 2) . . . . p. 189



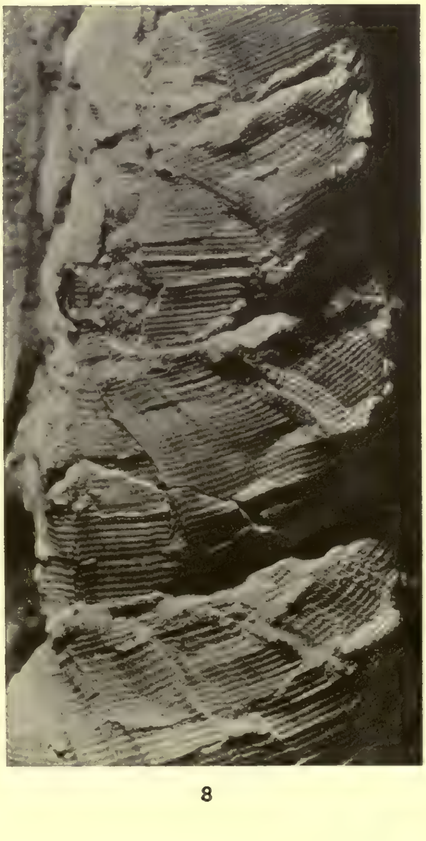
6



7



9



8

TURRITELLA s.str., TURRITELLA (TORQUESIA)

PLATE 30

FIGS. 10, 11. *Turritella* (*Torquesia*) *granulata* J. de C. Sowerby. Albian, Greensand, Blackdown, Devon. Holotype. BM, 43667. ×2. Sowerby collection; figured J. de C. Sowerby 1827, pl. 565, fig. 1. . . . . p. 183

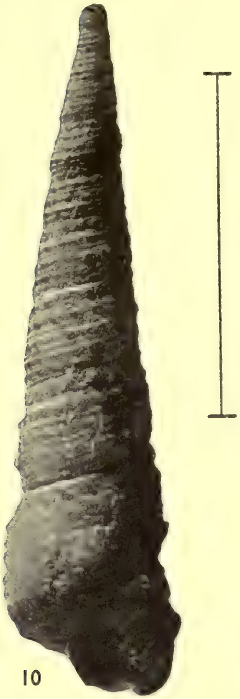
FIG. 12. Same species and locality. BM, G. 16149. ×2.

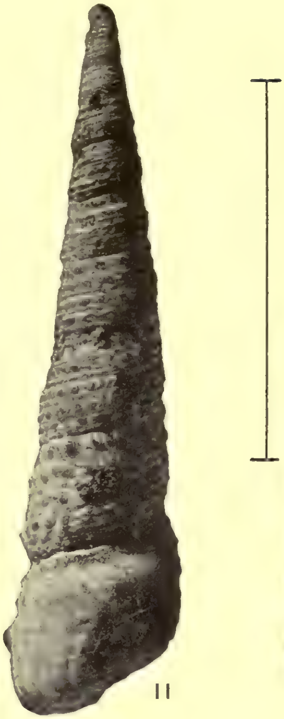
FIG. 13. Same species and locality. GSM, 93690. ×2.

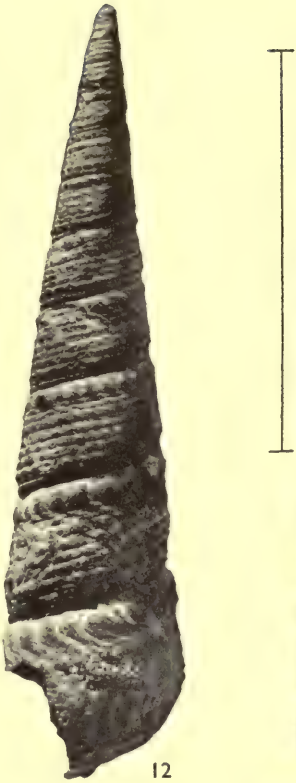
FIG. 14. Same species and locality; variety showing ornament of only four principal cords on later whorls (see p. 184). BM, G. 74108. ×2.

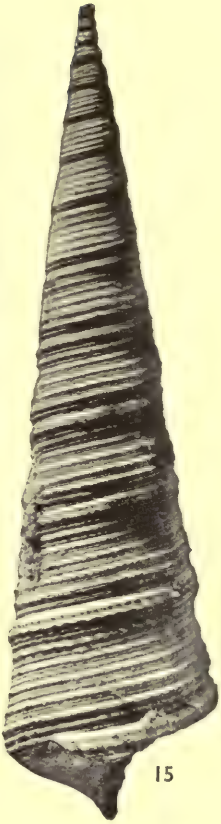
FIG. 15. *Turritella* (*Torquesia*) *faizai* sp. nov. Albian, Greensand, Blackdown, Devon. Holotype. SM, B. 44621. ×2 . . . . p. 188

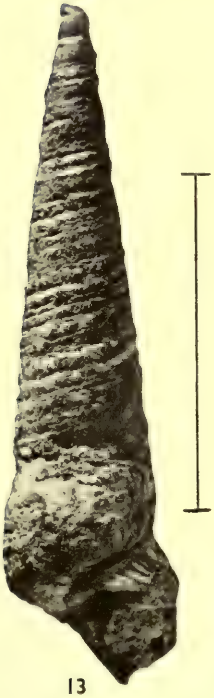
FIG. 16. *Turritella sherborni* sp. nov. Albian, Greensand, Blackdown, Devon. Holotype. BM, G. 74107. ×2 . . . . p. 190

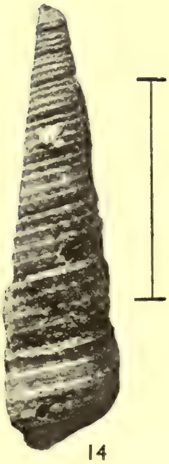

10

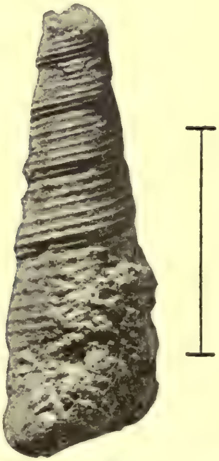

11


12


15


13


14


16

TURRITELLA (TORQUESIA), TURRITELLA s.lat.

PLATE 31

FIG. 17. *Turritella* (*Torquesia*) *vibrayeana* d'Orbigny. Albian, Gault, Folkestone, Kent. BM, G. 73790. ×2 . . . . p. 185

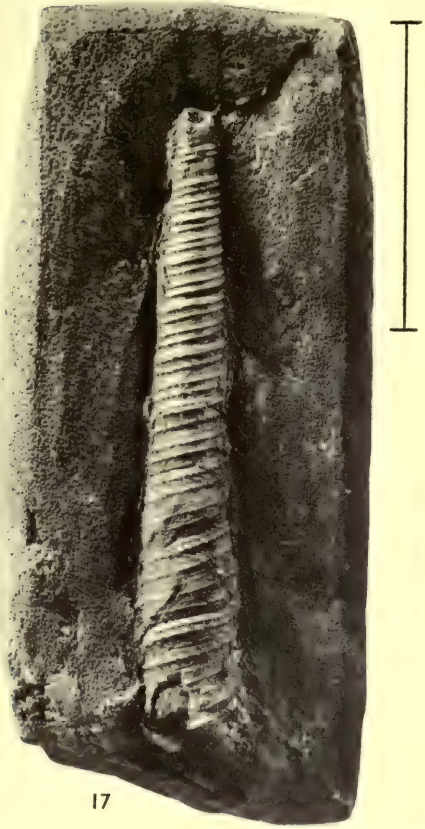
FIG. 18. Same species and locality. BM, G. 73791. ×2.

FIG. 19. Same species and locality. BM, G. 73784. ×2.

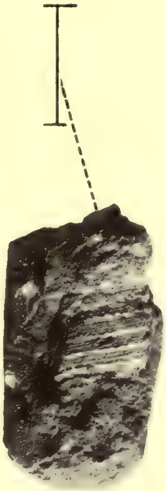
FIG. 20. Same species and locality. GSM, 93729. ×2.

FIG. 21. Same species and locality. GSM, 1703. ×2.

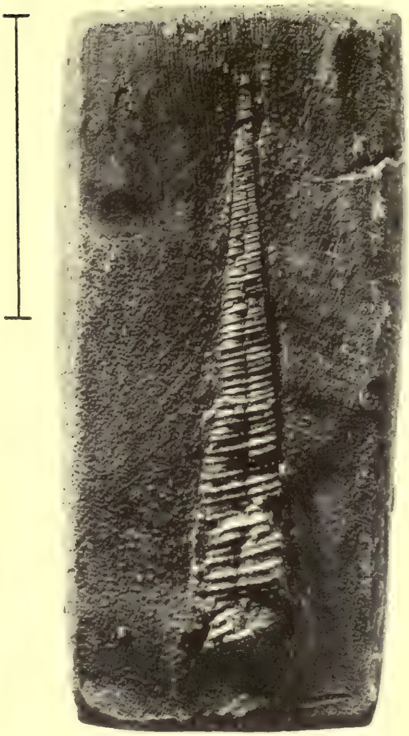
FIG. 22. Same species. Lower Gault, Fairy Dell, Stonebarrow Cliff, Charmouth, Dorset. BM, G. 49825. ×1½.



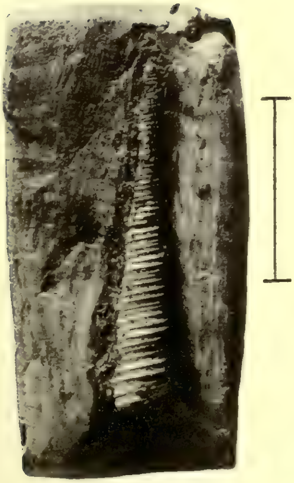
17



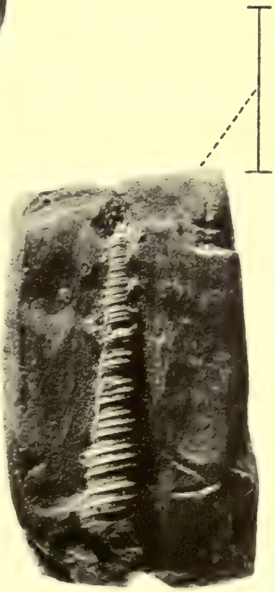
22



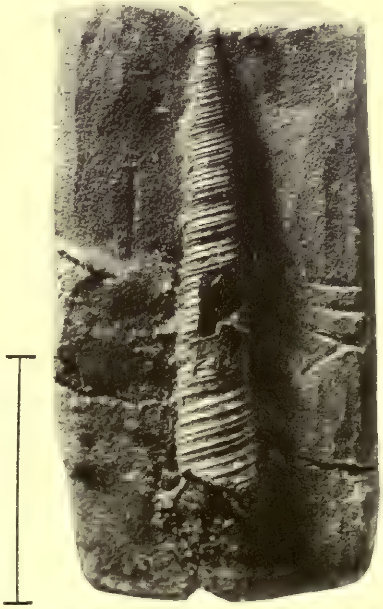
18



19



20



21

TURRITELLA (TORQUESIA)

PLATE 32

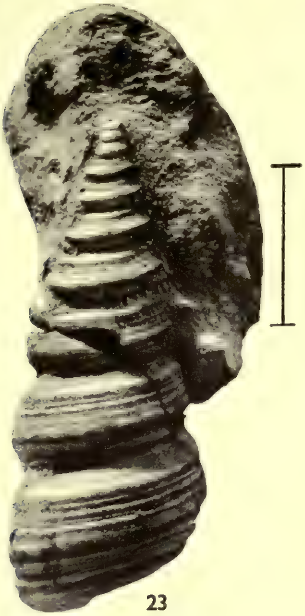
FIG. 23. *Mathilda coxi* sp. nov. Aptian, Lower Greensand, Atherfield Clay Series (bed known as the "Crackers"), near Atherfield, Isle of Wight. Holotype. SM, B. 27336. ×3 . . . . p. 191

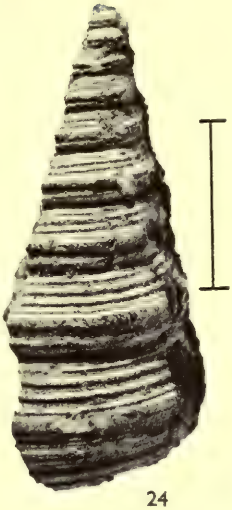
FIG. 24. *Mathilda ahmadi* sp. nov. Albian, Greensand, Blackdown, Devon. Holotype. SM, B. 44649. ×3 . . . . p. 193

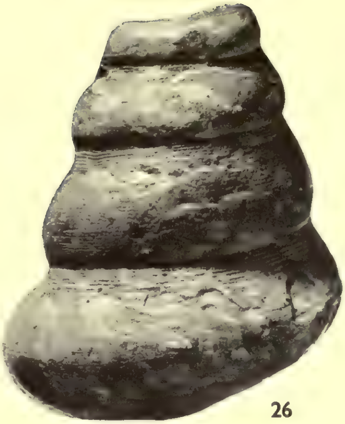
FIG. 25. *Turritella ageri* sp. nov. Albian, Greensand, Blackdown, Devon. Holotype. BM, G. 74106. ×2 . . . . p. 190

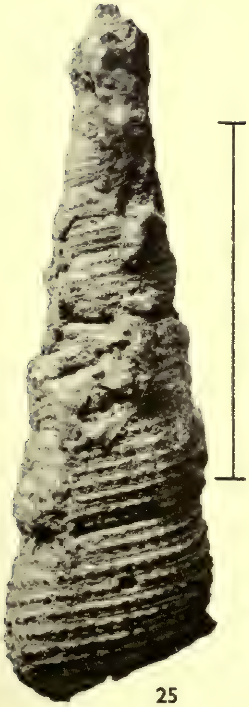
FIG. 26. "*Turritella*" *turbinata* J. de C. Sowerby. Cenomanian, Chalk Marl, Sussex. Holotype. BM, 44520. ×1. F. Dixon collection; figured J. de C. Sowerby *in* F. Dixon, 1850, pl. 29, fig. 2 . . . . p. 193

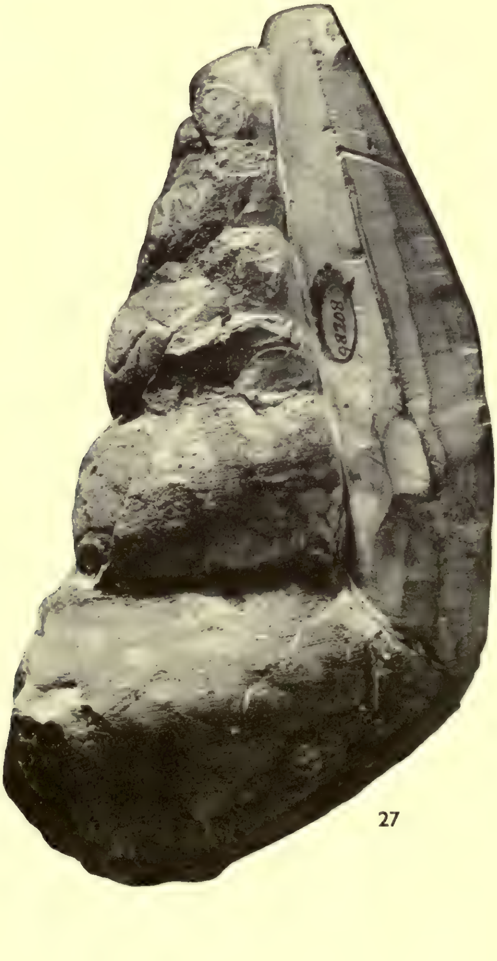
FIG. 27. Same species. Cenomanian, Chalk Marl, Ventnor, Isle of Wight. BM, 98208. ×1.


23


24


26


25


27

MATHILDA, TURRITELLA s.lat., "TURRITELLA"

PRINTED IN GREAT BRITAIN BY
ADLARD AND SON, LIMITED,
BARTHOLOMEW PRESS, DORKING

M. A. O.

THE MORPHOLOGY OF *TUBICAULIS AFRICANUS* SP. NOV. A FOSSIL FERN FROM TANGANYIKA

HENRY SMITH HOLDEN
AND
WILLIAM N. CROFT

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 7 No. 7
LONDON: 1962

THE MORPHOLOGY OF *TUBICAULIS AFRICANUS* SP. NOV. A FOSSIL FERN FROM TANGANYIKA

BY

HENRY SMITH HOLDEN and the late WILLIAM N. CROFT

Pp. 197–211 ; *Plates* 33–36 ; 16 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 7 No. 7
LONDON : 1962

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

This paper is Vol. 7, No. 7 of the Geological (Palaeontological) series.

© Trustees of the British Museum 1962

PRINTED BY ORDER OF THE TRUSTEES OF
THE BRITISH MUSEUM

Issued December 1962 *Price Eleven shillings*

THE MORPHOLOGY OF *TUBICAULIS AFRICANUS* SP. NOV. A FOSSIL FERN FROM TANGANYIKA

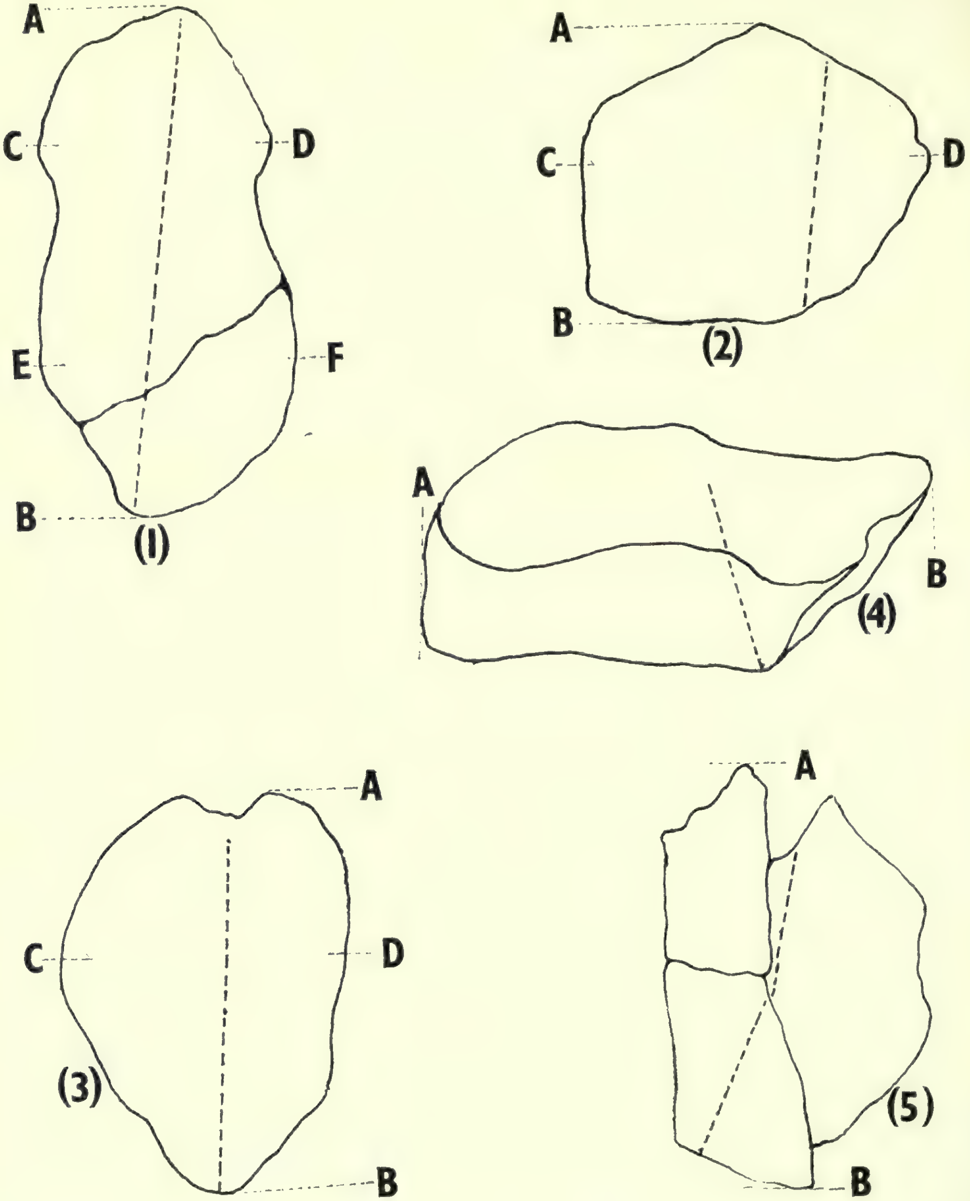
By HENRY SMITH HOLDEN & WILLIAM NOBLE CROFT

SYNOPSIS

The paper describes the morphology of a new species of fossil fern from the Ruhuhu area of Tanganyika. This is assigned to the genus *Tubicaulis* as *T. africanus* sp. nov. The relationships between the new species and the other fossil ferns assigned to the same genus and to possibly allied fossils are discussed.

INTRODUCTION

The stratigraphy of the Ruhuhu area of south-western Tanganyika and its correlation with the Karroo formations of South Africa have been the subject of detailed study both by Stockley (1931, 1932, 1947) and Nowack (1937). Stockley's investigations resulted in the collection of numerous animal and plant fossils among which the silicified fern stems and their attached roots and leaf bases forming the subject of this study were included. They were discovered by Charles Kirchstein, who was at that time Stockley's Field Assistant, lying in a restricted area on the surface slope of an exposure of Upper Permian age. In this area there is a local disconformity between the Upper Permian strata and the scarp of the overlying Triassic Kingori Sandstones and, although it is possible that the specimens could have been dislodged from pockets in the sandstone, Stockley, who was consulted with regard to this possibility, regarded such derivation as improbable. Inevitably, there must be some doubt, however, as to whether the specimens are of Upper Permian or Lower Triassic age. They were sent, with other fossils, to the Department of Palaeontology of the Natural History Museum and a considerable amount of preliminary work on them was undertaken by the late W. N. Croft. The pressure of other duties and the increasing ill-health which ultimately led to his death resulted in their being put aside and they were not the subject of further study until the latter part of 1959 when Dr. E. I. White, Keeper of the Department, kindly made available both the specimens and Croft's notes. The specimens, five in number, had been given a common Locality Number, S559, and additional distinguishing letters A to E. They are now registered as V.44725–29 in the Department of Palaeontology. Croft made outline sketches of the specimens indicating their dimensions and these are reproduced as Text-figures 1–5. It will be seen from these that specimen V.44729 was broken into several pieces when received and that a deep crack was present on one face of specimen V.44725. Two of the specimens, V.44725 and V.44727, are illustrated in Pl. 33, figs. 1, 2 and it is clear from a surface examination of these and the other specimens that this fern possessed an upright stem which was surrounded



FIGS. 1–5. *Tubicaulis africanus* sp. n. Outline sketches of the five specimens as originally received indicating their dimensions. Fig. 1 is the holotype, Figs. 2–5 are the paratypes. The heavy broken line in each of the figures indicates the position of the stele. Not drawn to scale.

Fig. 1, Holotype, V.44725, A–B 20·2 cms., C–D 13·3 cms., E–F 13·2 cms. ; Fig. 2, V.44726, A–B 9·3 cms., C–D 10·8 cms. ; Fig. 3, V.44727, A–B 11·9 cms., C–D 9·7 cms. ; Fig. 4, V.44728, A–B 16·5 cms. ; Fig. 5, V.44729, A–B 11·5 cms.

by a thick armour of persistent leaf bases. Trial sections indicated that, as so frequently happens in silicified material, the quality of the preservation of the tissues varied considerably from one part of any given specimen to another and that the more delicate tissues of the fossil frequently were replaced, partly or wholly, by non-structural matrix. This replacement was notably the case in specimen V.44727. The plant tissues, when examined on a cut surface, were mostly light brown in colour and trial sections indicated that very little carbon had been preserved in them. Because of this, attempts to obtain " peels " by smoothing and subsequent etching with hydrofluoric acid often gave very unsatisfactory results, the action of the acid being uneven and resulting in the production of " ghost peels " in which either the structural details of the plant tissues were lost or some or all the tissues were missing completely. During the course of the investigation attempts were made also to obtain " peels " both of *Tubicaulis solenites* and *Grammatopteris baldaufi* for comparison with the new fern but etching with hydrofluoric acid proved equally unsuccessful with these also. An exception to the lack of success attending etching techniques was provided, however, by specimen V.44729 which yielded a number of good quality " peels ". The information obtained from these was amplified by the examination of occasional successful " peels " from some of the other specimens together with ground sections and selected polished surfaces.

FILICALES

Family COENOPTERIDEAE

Genus ***TUBICAULIS*** Cotta, 1832 : 15

Tubicaulis africanus sp. nov.

(Plates 33–36 ; Text-figs. 1–11, 15, 16)

DIAGNOSIS. A fossil fern : stem upright surrounded by dense armour of persistent leaf bases : stem stele cylindrical, protostelic with numerous exarch protoxylem groups and with medulla of mixed tracheids and parenchyma : pitting of tracheids multiseriate scalariform or, in narrower tracheids, scalariform : cortex wide with scattered nests of sclerotic cells : petioles developed in close spiral succession : petiole traces initially monodesmic, later dividing into three, arched abaxially with free margins incurved when fully developed : region between stem and persistent leaf bases filled with long, uniseriate, septate hairs : roots with stout diarch stele arising at or near free margins of leaf traces.

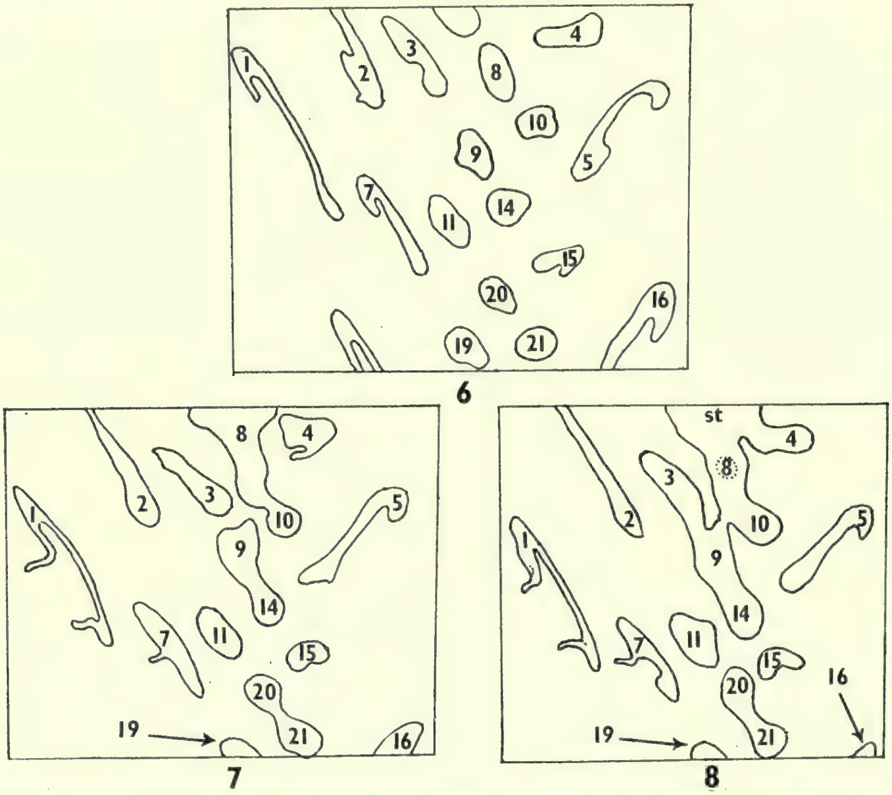
HOLOTYPE. Specimen V.44725 in the Department of Palaeontology, British Museum, (Natural History).

PARATYPES. Four specimens, V.44726–29, in the same Department.

LOCALITY. Ruhuhu area of south-western Tanganyika.

HORIZON. ? Upper Permian.

DESCRIPTION. *The Stem.* The surface tissues of the stem have not survived petrifaction and, as a consequence, it has proved impossible to determine its exact diameter but this ranges from approximately 4·5 cms. to 6·0 cms. Its centre is occupied by a small cylindrical stele which has a diameter of from 3·5 mm. to 4·0 mm. Its cylindrical character is somewhat obscured by the emission of a close succession of spirally arranged leaf traces showing a complex divergence (Pl. 34, fig. 3; Pl. 36, fig. 1). The stelar protoxylem is exarch and consists of a number of separate groups of small tracheids distributed around the periphery of the stele (Pl. 34, fig 3; Pl. 35. fig. 3). The majority of these possess scalariform pitting although, occasionally, they show suggestions of close spiral thickening. The metaxylem tracheids form a continuous hollow cylinder which varies somewhat in depth and which encloses a " mixed pith " consisting of a parenchymatous ground mass among which tracheids are scattered singly or in small groups (Pl. 34, fig. 3; Pl. 35, figs. 1, 2). The medullary parenchyma is not sharply delimited from the main mass of the metaxylem but extends into it in the form of small groups or radial plates of cells which may penetrate locally almost to the outer margin of the stele and even into the bases of the departing leaf traces (Pl. 35, fig. 4). The type of pitting of the metaxylem is often difficult to determine owing to imperfect preservation but, where this is sufficiently good, it is seen to consist of a single row of trans-

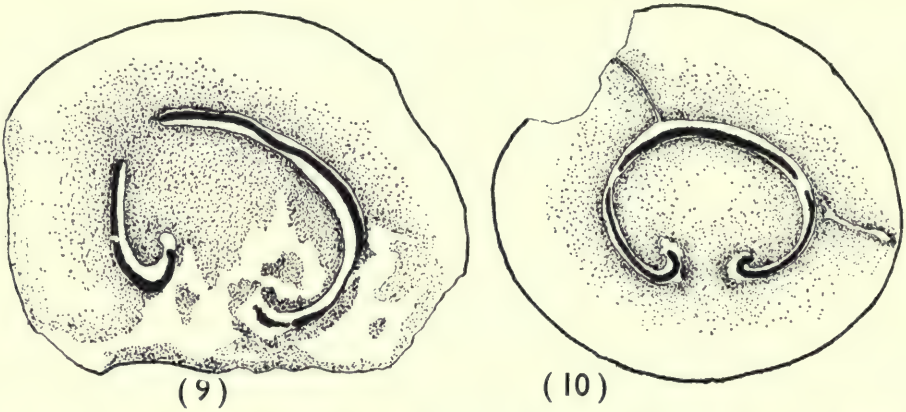


Figs. 6–8. *Tubicaulis africanus* sp. n. Outline sketches of portions of three longitudinal " peels " from V.44729. Fig. 6 (Peel 11, V.44729(13)), Fig. 7 (Peel 13, V.44729 (14)), Fig. 8 (Peel 14, V.44729(15)), showing the close succession of the petiole traces and the temporary vascular linkage of some of these. The petiole traces are numbered in the order of their emission from the stele.

versely elongated pits in the narrower tracheids whilst the wider ones possess two or three similar rows. The pitting is thus of the type termed multiseriate scalariform by Delevoryas & Morgan (1952). Most of the medullary tracheids are spindle shaped with pitting similar to that of the rest of the metaxylem although shorter tracheids with truncated ends are not uncommon, (Pl. 35, fig. 2). The phloem and its associated parenchyma have usually not been preserved and, at the best, are represented by shreds of pale brown tissue in which no structural features can be made out.

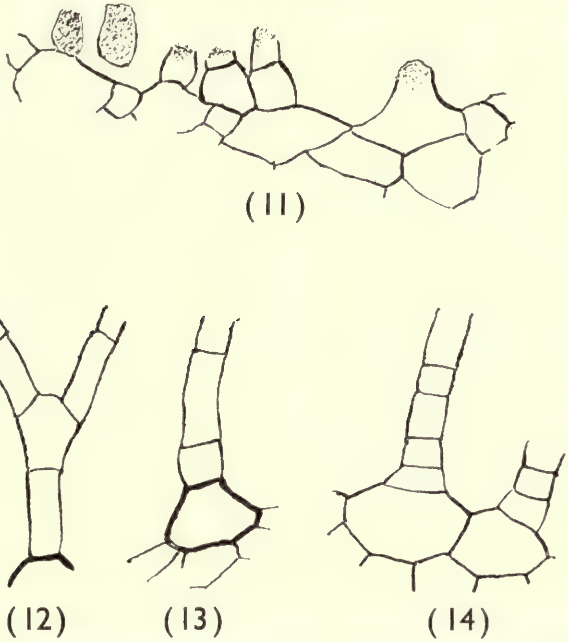
Scattered through the wide cortex are abundant groups of thick-walled cells forming sclerotic nests (Pl. 34, fig. 3 ; Pl. 35, fig. 1 ; Pl. 36, fig. 1), the component cells of which have dark contents. Some of these sclerotic nests have an attached fringe of parenchyma and are linked occasionally by similar groups of thin-walled cells. No continuous areas of parenchymatous ground tissue have been preserved although this does not appear to have led to any great spatial disturbance of the petiole and root traces traversing the stem cortex. The groups of sclerotic cells are frequently closely associated with these traces although this may be due, in part, to the loss of the cortical parenchyma.

The petiole. As already stated, the petiole traces are given off from the stem stele in close spiral succession and, as they begin to emerge from the outer tissues of the stem cortex, they produce in this an irregular series of superficial corrugations (Pl. 34, fig. 2). This crowded spiral succession may result also in a temporary vascular linkage between neighbouring petiole traces near the region of their emergence from the stem and is illustrated in Pl. 35, fig. 5 and, in outline, in Text-figs. 6–8. They develop a well-marked abaxial curvature immediately (Pl. 35, fig. 3) with the protoxylem tracheids forming a series of separate groups distributed along the convex adaxial surface. This distribution of the protoxylem is well shown not only in transverse sections of the petiole (Pl. 35, fig. 3) but also in tangential sections passing through the petiolar bundle at right angles to the sagittal plane immediately after it leaves the stem stele (Pl. 35, figs. 4, 5). Closely associated with each petiole trace is an oval mass of sclerotic cells which occupies its abaxial concavity. A continuation of this particular mass becomes closely applied to the abaxial face of the petiole trace as it moves outwards and forms a continuous strip along the whole abaxial face of the trace during its passage through the outer cortex of the stem. Similar groups of sclerotic cells are distributed also along the convex adaxial face of the trace and, near its point of origin, often form a more or less continuous band. Scattered irregularly through the strips of sclerotic cells which accompany the petiole traces are large ovoid cells which occur singly or in groups of two or three (Pl. 36, fig. 4). They are readily distinguished from the surrounding tissues by their larger size and by the absence of dark contents. They recall the elements described by C. Eg. & P. Bertrand (1911) as occurring in the inner cortex of *Tubicaulis berthieri* and which are interpreted by them as glandular cells. The petiole trace, during its passage outwards, takes a sharp upward course through the stem cortex. As it enters the base of the petiole, however, its upward curvature becomes much less pronounced so that, from the time of its inception to its later stages, the trace has the form of a sigmoid curve. During its transit, the abaxial curvature of the petiolar trace becomes steadily more pronounced with its free margins strongly recurved so that, when it enters the petiole, the xylem, in transverse section, has the shape of a slender letter C. (Pl. 36, fig. 1). The basal part of the petiolar cortex contains numerous scattered sclerotic nests and similar tissue, several cells in depth, forms a continuous layer immediately below the epidermis. This last, if preserved at all, is usually represented by a pale yellowish layer in which the cellular structure is lost. As the petiole moves further away from the stem, the sclerotic nests diminish in number and tend to disappear completely whilst the cortical tissues become homogeneous and are composed of small, somewhat thick-walled, cells apart from the continous layer of sclerenchyma lying just below the epidermis. This stage appears to be reached only in the more distal parts of the persistent leaf bases. At the same level, extramarginal gaps are sometimes developed in the petiolar xylem. These gaps may occur initially on one side only or they may arise symmetrically on either flank of the trace (Text-figs. 9, 10). When the first examples of these gaps were found it was thought they might be artefacts which had resulted from locally imperfect petrifaction but further investigätion showed that they were a normal feature in which the division of the xylem of the petiole trace was followed by its separation into three independent strands with the cortical tissues passing through the gaps between them. Whilst these gaps in the petiolar vascular supply resemble those resulting from the emission of extramarginal pinna-traces, it should be pointed out that none of the petioles examined shows any indication of the existence of such traces, although it is conceivable that they may develop from the contiguous margins of the xylem gaps or from the central bar at a higher level. However, no evidence of this has been found. A similar division of an initially monodesmic leaf trace is not uncommon in existing ferns (Davie, 1914),



FIGS. 9–10. *Tubicaulis africanus* sp. n. Camera lucida sketches of sections of two petioles. Fig. 9 from V.44726*j* shows, on the left, the complete division of the petiole trace and the separation of the distal part from the rest by cortical tissue and, on the right, the thinning of the xylem preparatory to division. Fig. 10 from V.44726*k* shows the symmetrical division of the petiole trace into three. Xylem in solid black, cortical tissues stippled (Both ×8).

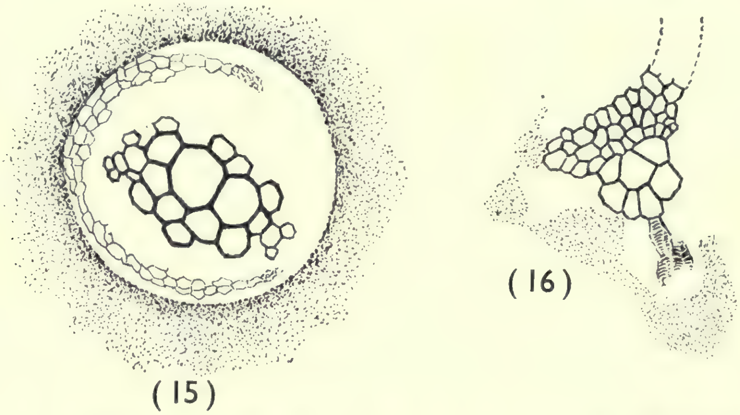
typical examples being those of *Cibotium barometz* and *Saccoloma elegans*. Although the adaxially curved petiole trace in both these ferns is more elaborate than that of *Tubicaulis africanus* both show a transient division into three meristeles, one median and two lateral, prior to their further sub-division (Bower, 1923; Davie, 1914; Gwynne-Vaughan, 1903). The persistent petiole bases are embedded in a dense mass of long uniseriate hairs through which the roots pass to the exterior (Pl. 36, fig. 3). Although the preservation of these hairs is imperfect, there are indications



Figs. 11–14. Fig. 11, *Tubicaulis africanus* sp. n. Portion of the petiolar epidermis showing the bases of several hairs, V.44726*j*. (×300). Figs. 12, 13, Bases of two hairs of *Cibotium regale* showing the thickened basal cell and, in 12, a bifurcation near the base (×150). Fig. 14, Bases of two hairs from *C. barometz* (×150).

that, like those found in many existing ferns, they were multicellular. Some of them arise from the basal parts of the petiolar epidermis and appear to develop from a single basal cell (Text-fig. 11) but it seems probable that many were developed also from the surface tissues of the stem. The existence of such surface hairs as distinct from flattened scales is widespread among palaeozoic ferns and they occur also in many existing ferns which are regarded as retaining other primitive characters (Bower, 1926). Comparatively short uniseriate hairs arising from a single basal cell form a thick covering to the rhizomes and petiole bases of *Matonia pectinata* (Seward, 1899). Those occurring in *Tubicaulis africanus*, however, are longer and appear to resemble more closely the long, brownish or golden yellow hairs which form a dense thatch clothing the stem apices and young petioles of various species of *Cibotium* such as *C. barometz* and *C. regale*. The hairs in these two species are somewhat coarser than the ones present in *Tubicaulis africanus* although, like them, they arise from a single basal cell. (Text-figs. 12–14). In *Cibotium regale*, however, several examples have been noted in which the hairs divide into two equal branches near the base (Text-fig 12). The basal cell in this species has thicker walls than the remaining cells of which the hair is composed and, when the hair is shed, this basal cell persists as a large, convex, golden-yellow boss which stands out prominently from the smaller epidermal cells which surround it.

Roots. The roots arise on or near the free incurved margins of the petiole traces (Pl. 35, fig. 6 ; Text-fig. 16), usually in pairs, one from each margin. No evidence has been found indicating that they develop from the stem as well. As a rule, only the comparatively stout diarch stelar xylem of the root is preserved and this is surrounded by a sheath of dark sclerotic elements with a clear space between this and the root stele (Text-fig. 15). In this clear space but well separated from the stele, there are often traces of the other root tissues, these usually taking the form of a delicate complete or broken cylinder (Text-fig. 15). Occasionally, roots occur in which the whole of the cortical tissues have been partly petrified but, even here, the preservation is such that all that can be said is that they are parenchymatous. There is some evidence that the roots may branch whilst still within the stem cortex or among the hairs which enclose the persistent leaf bases. In a few instances, traces of the roots are found at the surface of the specimens and, where this is the case, these take the form of short oval rods or papillae representing the root steles.



Figs. 15, 16. *Tubicaulis africanus* sp. n. Fig. 15, T.S. of a root in the stem cortex showing the stout diarch stele and traces of the superficial tissues. The sclerotic tissue is stippled. V.44729(28). ×350. Fig. 16, The recurved margin of a petiole trace showing the origin of a root. Note the larger diameter of the tracheids of the root metaxylem compared with those of the petiole. The sclerotic tissue is stippled. V.44729(27). ×200.

Discussion. The seven species at present included in the genus *Tubicaulis* comprise ferns showing wide differences in habit, these ranging from the relatively small epiphytic forms such as *T. berthieri* and *T. scandens* to those like *T. solenites* and *T. africanus* which possessed stout upright stems enclosed in an armour of persistent leaf bases. This wide variation in habit is not, in itself, a valid reason for generic separation since a similarly wide variation in habit occurs in many existing fern genera. The genus *Asplenium*, for example, includes, in addition to both creeping and radially organised terrestrial species, minute epiphytes and massive specialised ones. They are included in the same genus by taxonomists in view of the agreement in their soral and sporangial characteristics. In the absence of the reproductive organs, however, palaeobotanists are compelled to rely solely on such morphological characters as are available in the specimens they study, this imposing a limitation which has been stressed already by Mamay (1952) and, more recently still, by Eggert (1959). A further handicap is often imposed by the small number of specimens which has been discovered and by their incomplete character, a handicap well-illustrated by *Tubicaulis* itself in which five of the seven species assigned to it have been described from single examples. In spite of these limitations, however, it seems reasonable, in the present state of our knowledge, to assign them provisionally to the same genus since all possess certain anatomical features in common, namely :

(a) An essentially terete, protostelic axial vascular system devoid of secondary thickening with exarch protoxylem groups and in which the protostele may be wholly tracheidal or possess a core of mixed tracheids and parenchyma ;

(b) petiole traces which depart from the stem stele, either as flat or slightly curved tangential bands which assume, ultimately, the shape of a letter C in transverse section and in which the curvature is abaxial, or in which the abaxial curvature is well-developed immediately on the separation of the petiole trace from the stem stele.

It will be noted that this definition of the essential generic vascular characteristics is slightly modified from that proposed by Mamay (1952) in the introduction to his description of *Tubicaulis scandens* and has been rendered necessary as a result of the discovery and description of other species subsequent to the publication of his paper.

The root systems of the various species provided no indications of common ancestry apart from the fact that the diarch steles are of the stout osmundaceous type rather than the slenderer type characteristic of existing leptosporangiate ferns. Like the roots of the fossil Osmundaceae, they show a wide variation in their source of origin (Kidston & Gwynne-Vaughan, 1907–14). Thus in *T. scandens* they arise solely from the stem (Mamay, 1952), in *T. sutcliffii* (Stopes, 1906), *T. multiscalariformis* (Delevoryas & Morgan, 1952) and *T. stewartii* (Eggert, 1959) they arise from the stems and basal parts of the petioles and in *T. africanus* from the petioles only.

Adequate knowledge of the nature of the pinna-traces is lacking also. Stopes (1906) records the presence of two small strands in the cortex of one of the petioles of *T. sutcliffii* which were, presumably, pinna-traces although their origin could not be determined. Mamay (1952) shows that, in *T. scandens*, the pinna-traces are paired and that they are slightly but definitely extramarginal in origin whilst, in *T. solenites* in which they are also paired and slightly extramarginal, they bifurcate whilst still within the petiolar cortex, each branch supplying a separate pinna (Stenzel, 1889, pl. 1, figs. 4–9). Morgan & Delevoryas (1954), on the basis of information supplied by Nickerson, state that in *T. multiscalariformis* the pinnae are borne in two rows, one on either side of the petiole. Grateful acknowledgments are due to Dr. Nickerson who has kindly supplied " peels " from coal balls in the collection of the Washington University Department of Botany confirming this.

A point worthy of note is that in both *T. solenites* and *T. scandens* the departure of the pinna-trace does not appear to cause a break in the continuity of the main petiolar strand. In attempting to indicate affinities within the genus, we are thus left only with the stelar characters and those of the petiole traces. Judged by these characters, the seven species assigned to *Tubicaulis* fall into two groups, *T. solenites*, *T. sutcliffii*, *T. berthieri* and *T. scandens* all possessing a homogeneous, wholly tracheidal protostele and a leaf trace which, initially, has the form of a flat or slightly curved tangentially expanded bar, whilst *T. multiscalariformis*, *T. stewartii* and *T. africanus* are characterized by the development of intrastelar parenchyma, slight in amount in *T. multiscalariformis* (Eggert, 1959) but much more abundant in both *T. stewartii* and *T. africanus*. These three species also agree in possessing petiole traces in which the assumption of an abaxial curvature occurs at a very early stage. Although there is a close resemblance in vascular structure between *T. stewartii* and *T. africanus* and also in the fact that both possess a surface covering of closely set uniseriate multicellular hairs, they differ considerably in habit and in numerous other features and these differences, combined with the wide difference in geological age, rule out any suggestion that they may have been specifically identical.

The relationship of the seven species now included in the genus *Tubicaulis* to other palaeozoic ferns does not appear to be a close one. The genera which resemble *Tubicaulis* in possessing an abaxially curved petiole trace are *Psalixylon* (Holden, 1960), *Apotropteris* and, possibly, *Anachoropteris* (Morgan & Delevoryas, 1954). All these are readily distinguished anatomically from *Tubicaulis* by their petiolar vascular characters and the likelihood of any close relationship either with that genus or with each other seems remote. A recent paper by Hall (1961) has described for the first time a radially organised plant bearing typical *Anachoropteris involuta* petioles. The stem of this plant is protostelic with, probably, exarch protoxylem. The stelar xylem is not homogeneous but contains plates of parenchyma interspersed among the tracheids. The trend towards the replacement of tracheids by parenchyma in the centre of the stele (i.e. towards medullation) is of wide occurrence in both the ferns and also in the fossil lycopods and there seems no valid reason why this plant should not be assigned to the genus *Anachoropteris* in view of its petiolar anatomy.

The fact that an abaxially curved leaf trace occurs in ferns along several apparently unrelated or very distantly related lines of descent suggests that this type of leaf trace may well have arisen independently from different ancestral stocks.

Of the other palaeozoic fern genera, *Grammatopteris* has been the one considered to be nearest *Tubicaulis* (Scott, 1920) although this view is open to some doubt. Of the two species of *Grammatopteris* of which both stem and petiole are known, *G. rigolloti* has been studied by Renault (1891, 1896) and Corsin (1937) whilst the most recent investigation of *G. baldaufi* has been that of Sahni (1932). Both species possess an exarch protostele and, in both, the petiole trace has the form of a tangentially flattened bar which, in this respect, resembles that of those species of *Tubicaulis* in which the abaxial curvature of the petiole trace is, initially, slight or absent. Renault's account and figures of *Grammatopteris rigolloti* (Renault, 1891, 1896), although adequate for diagnostic purposes, left a number of features obscure and Corsin's more detailed study has served both to amplify Renault's account and to reveal additional points of interest. The most unexpected result of Corsin's work was that it demonstrated the presence in the holotype of a thin peripheral zone of secondary xylem surrounding the stem stele. This encloses a solid mass of primary xylem composed entirely of tracheids of varying diameter in which the pits apart from the protoxylem were multiseriate.

Renault's co-type was a small, thick preparation which showed no trace of secondary xylem. The tissues forming the core of the stele are imperfectly preserved but Corsin interpreted them as probably representing the pith, an interpretation which receives support from the two additional sections prepared from " le culot de taille " in which the presence of intrastelar parenchyma is undoubted. Corsin considered that the differences between the type section and the others were due to their being cut at different levels, the type being from nearer the base than the co-type and the additional sections (Corsin, 1937 : 52).

The petiole trace of *G. rigolloti*, although it shows a general resemblance to that of some species of *Tubicaulis* (e.g. *T. solenites*, *T. scandens*), differs in a number of details. Briefly, these are (a) that the protoxylem is confined to two slightly adaxial groups occupying the opposite margins of the trace, (b) that the slight curvature seen in the more distal parts of the trace is adaxial, and (c) that the pinna-traces are marginal in origin.

The specimens of *Grammatopteris baldaufi* do not appear to be so well preserved as those of *G. rigolloti* but it seems clear that the plant was also protostelic with a complete absence of intrastelar parenchyma but with a stellate core, most of which consisted of normal, elongated tracheids mixed with a small number of short, much wider ones (the " parenchymatous tracheids " of Sahni). The petiole trace is very like that of *G. rigolloti* with the protoxylem forming two groups, one at each end of the tangentially flattened xylem bar. The trace, in many instances, shows a slight adaxial curvature in the free petiole although this is possibly an artefact.

From the available data is seems clear that the relationship between *Tubicaulis* and *Grammatopteris* is not a particularly close one and that the genus *Tubicaulis*, as at present constituted, must continue to occupy a somewhat isolated position among the palaeozoic Filicales.

SUMMARY

Tubicaulis africanus is a fern probably of Upper Permian age which was discovered in the Ruhuhu area of Tanganyika. It possesses a stout, upright stem surrounded by a close armour of persistent leaf bases. The stem has a slender, cylindrical stele in which the protoxylem is exarch and in which the metaxylem consists of a peripheral, wholly tracheidal zone enclosing a core of mixed tracheids

and parenchyma. The wide cortex is characterized by abundant scattered nests of sclerotic cells with dark contents among which larger clear ovoid cells occur.

The petioles are given off in close spiral succession. The petiolar vascular supply is initially monodesmic with a distinct abaxial curvature which becomes steadily more pronounced distally and in which the free margins ultimately are recurved. The numerous protoxylem groups are distributed along the whole of the adaxial surface of the trace. The region between the surface of the stem and the petiole bases is packed with long uniseriate hairs.

The roots, which arise at and near the margins of the petiole traces, are diarch with a stout stele resembling that of the zygopterids and Osmundaceae.

ACKNOWLEDGEMENTS

Grateful acknowledgements are due to Dr. E. I. White, Keeper of the Department of Palaeontology, for placing the specimens of *Tubicaulis* at my disposal and for facilities for their study. I am indebted also to Mr. F. M. Wonnacott of the Department for several helpful suggestions. I am further indebted to Dr. W. Dean for the photograph reproduced in Plate 34, fig. 1. The expert assistance of the staff of the Photographic Department has been invaluable and all the remaining figures in Plates 33–36 are from negatives and prints supplied by them.

REFERENCES

BERTRAND, C.-Eg. & P. 1911. Le *Tubicaulis berthieri* (sp. nov.). *Bull. Soc. Hist. nat. Autun*, **24** : 43–92, pls. 1–3.

BOWER, F. O. 1923. *The Ferns (Filicales)*, **1**. *Analytical Examination of the Criteria of Comparison*. 350 pp., 307 figs. Cambridge.

—— 1926. The Dermal Appendages of the Ferns. *Ann. Bot.*, London, **40** : 479–490.

CORSIN, P. 1937. *Contribution à l'étude des Fougères anciennes du Groupe des Inversicatenales*. 247 pp., 42 pls. Lille.

COTTA, C. B. 1832. *Die Dendrolithen in Beziehung auf ihren innern Bau.* ix + 89 pp., 20 pls. Dresden & Leipzig.

DAVIE, R. C. 1914. The Pinna-Trace in the Ferns. *Trans. Roy. Soc. Edinb.*, **50** : 349–378, pls. 33–35.

DELEVORYAS, T. & MORGAN, J. 1952. *Tubicaulis multiscalariformis* : a new American coenopterid. *Amer. J. Bot.*, Lancaster, **39** : 160–166, 15 figs.

EGGERT, D. A. 1959. Studies of palaeozoic ferns : *Tubicaulis stewartii* sp. nov. and evolutionary trends in the genus. *Amer. J. Bot.*, Lancaster, **46** : 594–602, 14 figs.

GWYNNE-VAUGHAN, D. T. 1903. Observations on the Anatomy of Solenostelic Ferns, Pt. 2. *Ann. Bot.*, London, **17** : 689–742, pls. 33–35.

HALL, J. 1961. *Anachoropteris involuta* and its attachment to a *Tubicaulis* type of stem from the Pennsylvanian of Iowa. *Amer. J. Bot.*, Lancaster, **48** : 731–737, 11 figs.

HOLDEN, H. S. 1960. The Morphology and Relationships of *Rachiopteris cylindrica*. *Bull. Brit. Mus. (Nat. Hist.) Geol.*, London, **4** : 51–69, pls. 8–10.

KIDSTON, R. & GWYNNE-VAUGHAN, D. T. 1907–14. On the Fossil Osmundaceae, Pts. I–V. *Trans. Roy. Soc. Edinb.*, **45** : 759–780, pls. 1–6 (1907) ; Pt. II, **46** : 213–232, pls. 1–4 (1908) ; Pt. III, **46** : 651–667, pls. 1–8 (1909) ; Pt. IV, **47** : 455–477, pls. 1–4 (1910) ; Pt. V, **50** :469–479, pls. 41–44 (1914).

MAMAY, S. H. 1952. An Epiphytic American Species of *Tubicaulis*. *Ann. Bot.*, London (n.s.) **16** : 145–162, pl. 9.

MORGAN, J. & DELEVORYAS, T. 1954. An anatomical study of a new coenopterid and its bearing on the morphology of certain coenopterid petioles. *Amer. J. Bot.*, Lancaster, **41** : 198–203, 9 figs.

NOWACK, E. 1937. Zur Kenntnis der Karroo Formation in Ruhuhu Graben (D.O.A.). *N. Jb. Min. Geol. Paläont.*, Stuttgart, **68**, B : 380–412, 7 figs.

RENAULT, B. 1891. Note sur la famille des Botryoptéridées. *Bull. Soc. Hist. nat. Autun*, **4** : 349–373, pls. 10, 11.

—— 1896. *Bassin Houiller et permien d'Autun et d'Epinac, IV. Flore Fossile II.* 578 pp., atlas, pls. 28–89. Paris.

SAHNI, B. 1932. On a Palaeozoic Tree-fern, *Grammatopteris baldaufi* (Beck) Hirmer, a Link between the Zygopterideae and Osmundaceae. *Ann. Bot.*, London, **46** : 863–877, pl. 35.

SCOTT, D. H. 1920. *Studies in Fossil Botany, I. Pteridophyta.* 3rd ed., xxiii + 434 pp., 190 figs. London.

SEWARD, A. C. 1899. On the Structure and Affinities of *Matonia pectinata*. *Philos. Trans.*, London (B) **191** : 171–209, pls. 1–3.

STENZEL, G. 1889. Die Gattung *Tubicaulis* Cotta. *Bibl. Bot.*, Cassel, **12** : 1–50, pls. 1–7.

STOCKLEY, G. M. 1931. Report on the Geology of the Ruhuhu Coalfield. *Tanganyika Geol. Surv. Bull.*, **2** : 1–63, pls. 1–6.

—— 1932. The Geology of the Ruhuhu Coalfield, Tanganyika Territory. *Quart. J. Geol. Soc. Lond.*, **88** : 610–622, pl. 38.

—— 1947. The Geology and Mineral Resources of Tanganyika Territory. *Bull. Imp. Inst. Lond.*, **45** : 375–406, pls. 1–4.

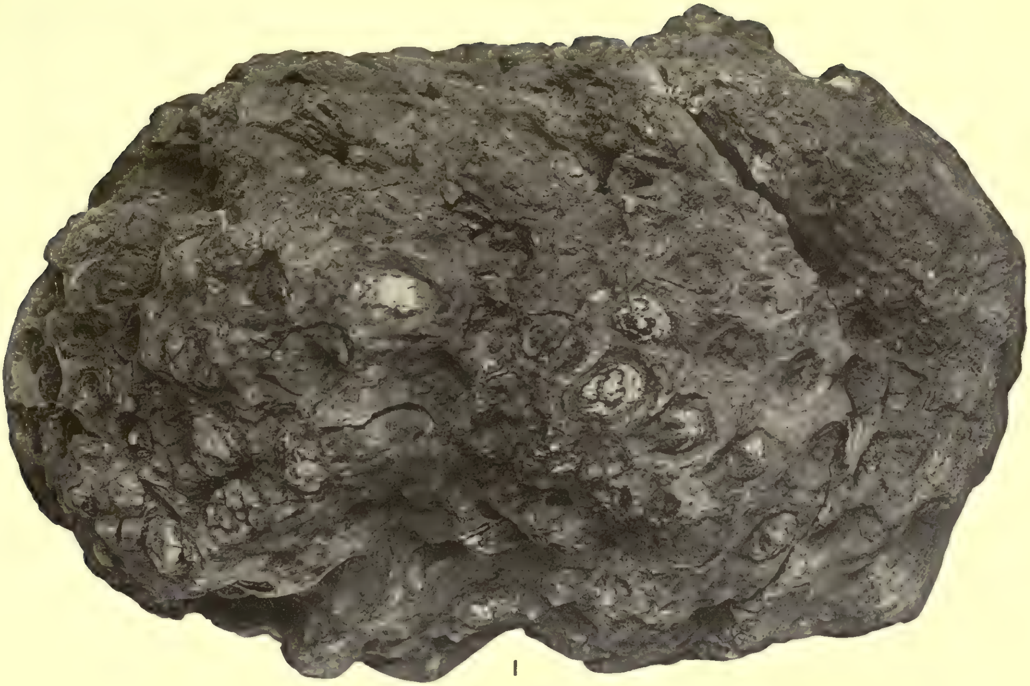
STOPES, M. C. 1906. A New Fern from the Coal Measures, *Tubicaulis sutcliffii* sp. nov. *Mem. Manchr. Lit. Phil. Soc.*, **50** : 1–34, pls. 1–3.

BRITISH MUSEUM NATURAL HISTORY

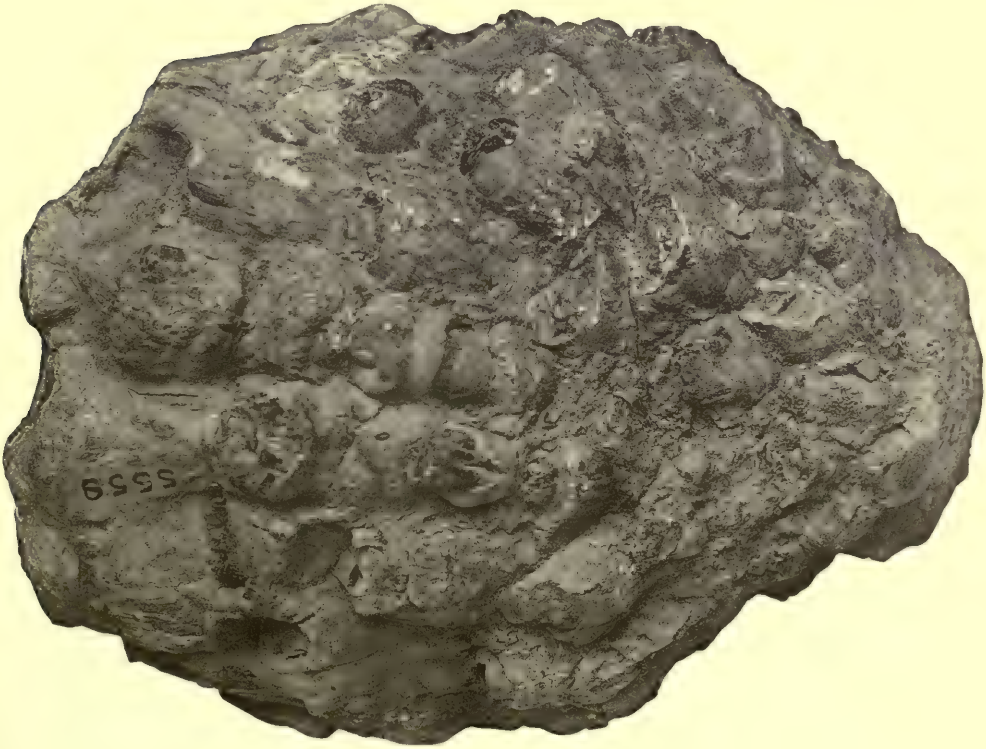
PLATE 33

Tubicaulis africanus **sp. n.**

FIG. 1. Holotype (V.44275). × $\frac{2}{3}$ approx.
FIG. 2. Another specimen, V.44727, slightly enlarged.



1



2

TUBICAULIS

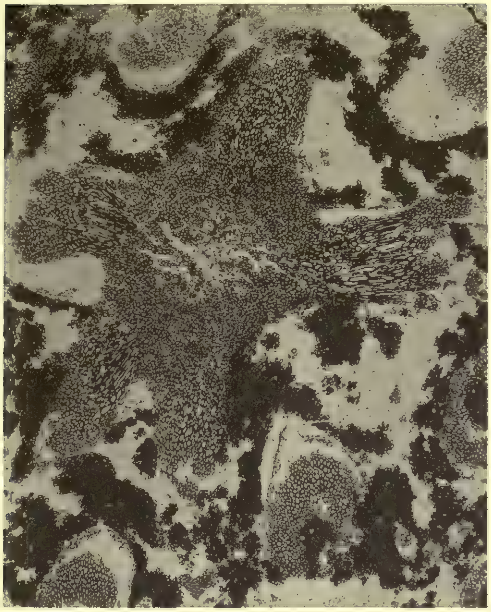
PLATE 34

Tubicaulis africanus sp. n.

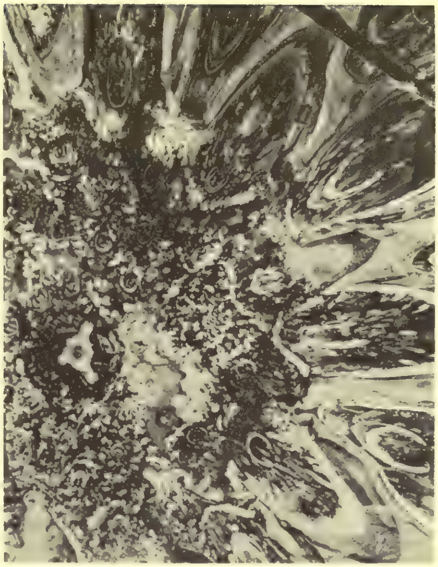
FIG. 1. Part of the smoothed and polished surface of a transverse section through V.44726*a* showing the armour of crowded, persistent leaf bases. About nat. size.

FIG. 2. Part of the smoothed and polished surface of a transverse section through V.44726*c* showing the stele and part of the stem cortex and leaf bases. (× 1·25).

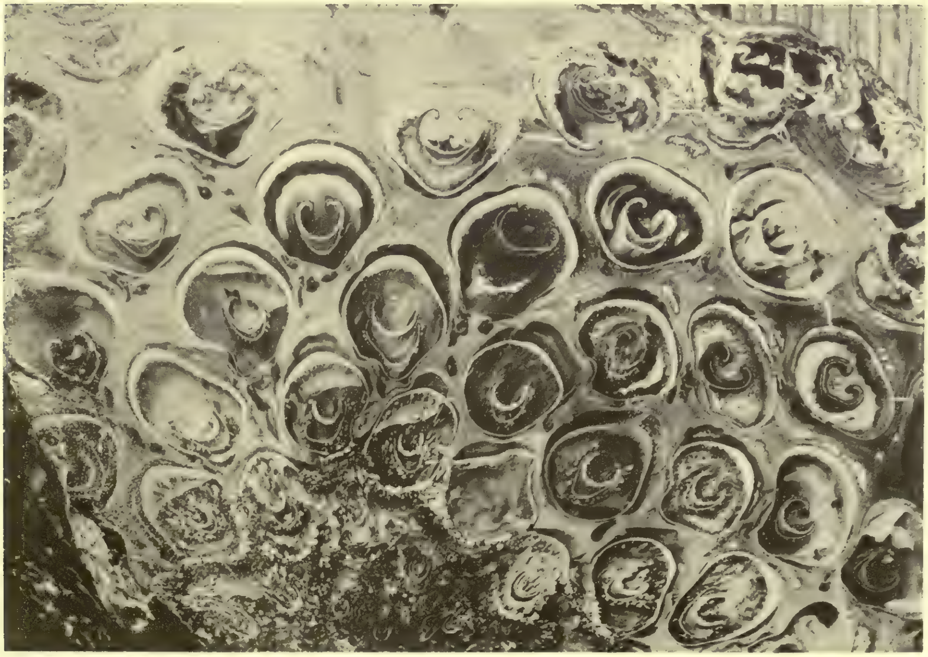
FIG. 3. T.S. of stele showing the " mixed pith " and five still attached leaf traces, V.44729 (28). (× 15).



3



2



1

TUBICAULIS

PLATE 35

Tubicaulis africanus sp. n.

FIG. 1. L.S. of stele showing the " mixed pith ", bases of leaf traces and patches of cortical sclerenchyma. V.44729(21). Longitudinal series No. 25. (×15).

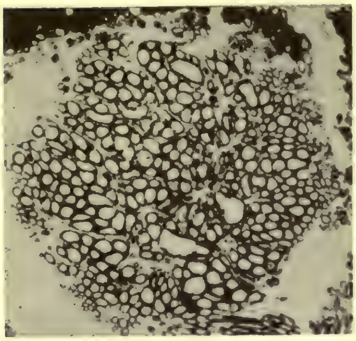
FIG. 2. L.S. of part of stele more highly magnified. V.44729(24). Longitudinal series No. 30. (×30).

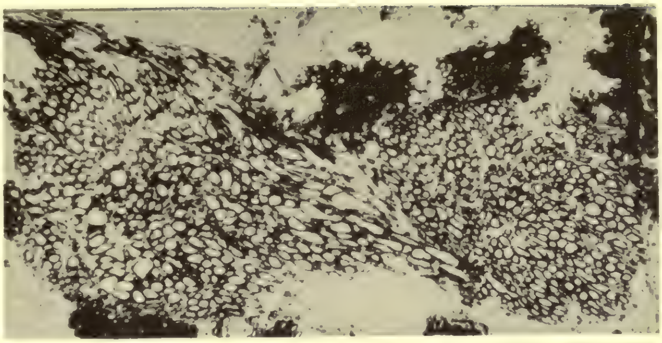
FIG. 3. T.S. of a leaf trace at the point of departure from the stele, V.44729(25). (×20).

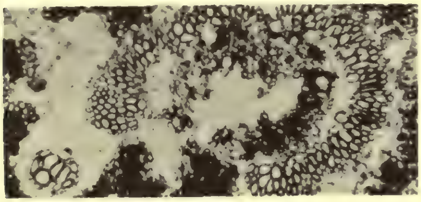
FIG. 4. Tangential section of a leaf trace showing the peripheral protoxylem groups, V.44729(13). (×25).

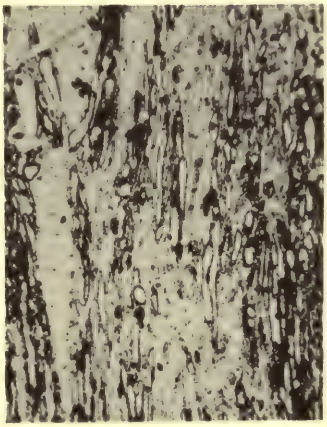
FIG. 5. Tangential section of two leaf traces showing their temporary vascular linkage, V.44729(14). (×20).

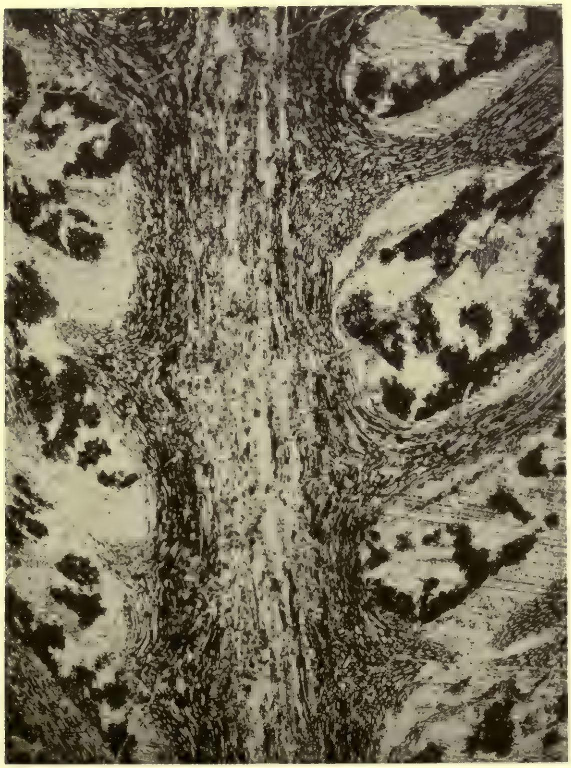
FIG. 6. T.S. of a leaf trace in the stem cortex from which a root trace has just been given off, V. 44729(25). (×15).

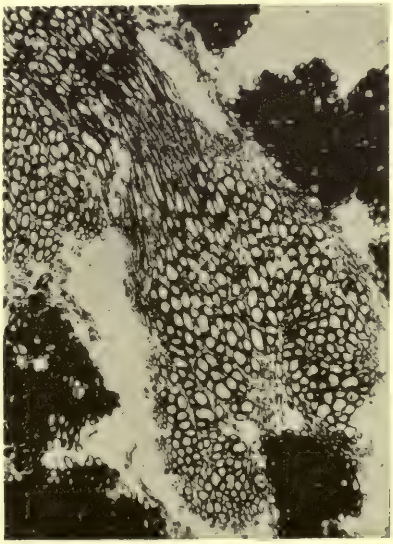

4


5


6


2


1


3

TUBICAULIS

PLATE 36

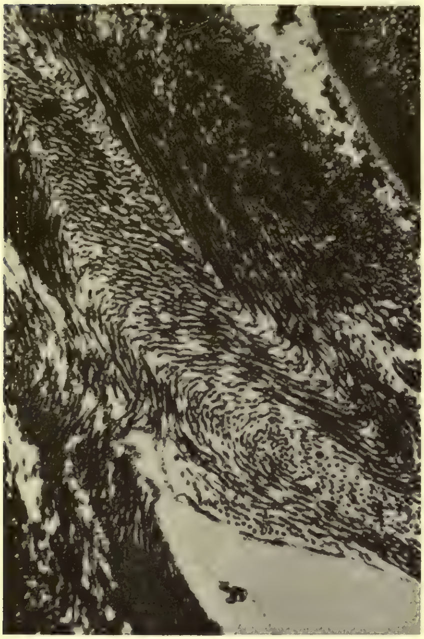
Tubicaulis africanus sp. n.

FIG. 1. Tangential section through the stem cortex showing the crowded leaf traces and the scattered areas of sclerenchyma, V.44729(13). (× 30).

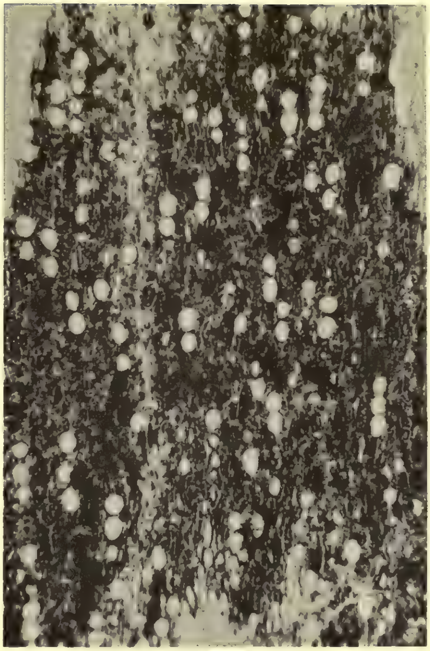
FIG. 2. T.S. of a fully developed leaf trace, V.44729(31). (× 12).

FIG. 3. Part of the area between two petioles showing the packing of hairs, V.44726*j*. (× 30).

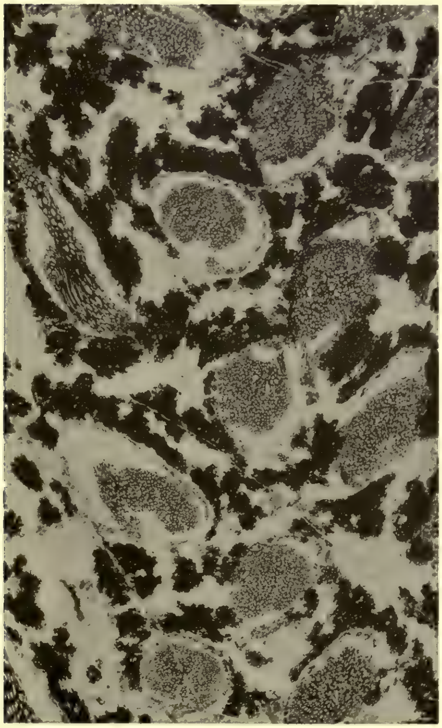
FIG. 4. An area of petiolar cortical sclerenchyma in L.S. showing the groups of " clear " cells, V.44729(30). (× 30).



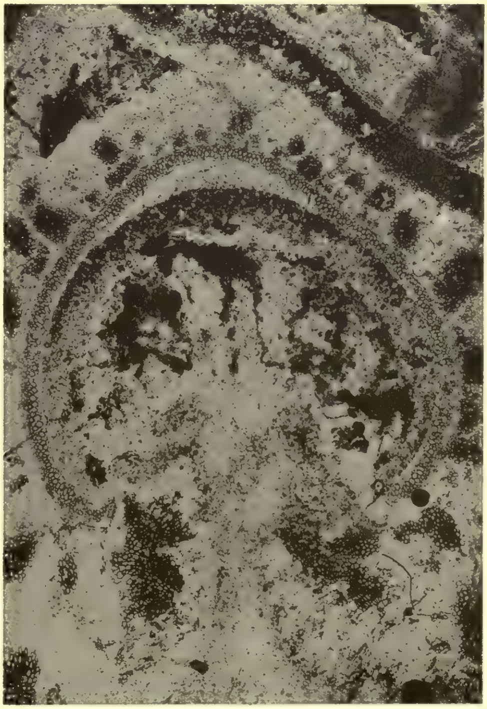
3



4



1



2

TUBICAULIS

BRITISH MUSEUM NATURAL HISTORY

.H.C.

THE ORDOVICIAN TRILOBITE FAUNAS OF SOUTH SHROPSHIRE, III

W. T. DEAN

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 7 No. 8
LONDON: 1963

THE ORDOVICIAN TRILOBITE FAUNAS OF SOUTH SHROPSHIRE, III

BY

WILLIAM THORNTON DEAN

Pp. 213–254; *Pls.* 37–46

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 7 No. 8
LONDON: 1963

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

This paper is Vol. 7, No. 8 of the Geological (Palaeontological) series.

© Trustees of the British Museum 1963

PRINTED BY ORDER OF THE TRUSTEES OF
THE BRITISH MUSEUM

Issued February, 1963 *Price Thirty Shilling*

THE ORDOVICIAN TRILOBITE FAUNAS OF SOUTH SHROPSHIRE, III

By WILLIAM THORNTON DEAN

SYNOPSIS

This paper is the third of a series of four dealing with the Caradoc trilobites of south Shropshire. Those described belong to fifteen genera or subgenera, of which one, *Remopleurella*, is new, and twenty-six species or subspecies, of which five are new. The trilobites comprise the gonatoparian family Calymenidae, together with all the known opisthoparian forms, belonging to nine families.

CONTENTS

	Page
I. SYSTEMATIC DESCRIPTIONS	216
Family Calymenidae Burmeister	216
Flexicalymene acantha Bancroft	216
Flexicalymene caractaci (Salter)	217
Flexicalymene planimarginata (Reed)	217
Flexicalymene cobboldi sp. nov.	218
Flexicalymene (*Reacalymene*) *pusulosa* (Shirley)	220
Flexicalymene (*Reacalymene*) cf. *limba* (Shirley)	221
Flexicalymene (*Reacalymene*) *horderleyensis* sp. nov.	221
Onnicalymene onniensis (Shirley)	223
Onnicalymene laticeps (Bancroft)	224
Onnicalymene salteri (Bancroft)	224
Gravicalymene praecox (Bancroft)	225
Gravicalymene inflata sp. nov.	227
Family Asaphidae Burmeister	229
Subfamily Asaphinae Burmeister	229
Parabasilicus powisi (Murchison)	229
Family Illaenidae Hawle & Corda	233
Subfamily Illaeninae Hawle & Corda	233
Illaenus cf. *fallax* Holm	233
Family Lichidae Hawle & Corda	234
Subfamily Lichinae Hawle & Corda	234
Metopolichas ? sp.	234
Subfamily Homolichinae Phleger	235
Platylichas laxatus (M'Coy)	235
Family Odontopleuridae Burmeister	237
Subfamily Odontopleurinae Burmeister	237
Primaspis harnagensis (Bancroft)	237
Primaspis caractaci (Salter)	239
Family Olenidae Burmeister	241
Subfamily Triarthrinae Ulrich	241
Triarthrus cf. *linnarssoni* Thorslund	241
Family Otarionidae R. & E. Richter	242
Subfamily Otarioninae R. & E. Richter	242
Otarion sp.	242

Family Proetidae Salter 243
Subfamily Proetidellinae Hupé 243
Proetidella fearnsidesi Bancroft 243
Proetidella? sp. 246
Family Remopleurididae Hawle & Corda 246
Subfamily Remopleuridinae Hawle & Corda 246
Remopleurides warburgae sp. nov. 246
Remopleurides latus Olin *onniensis* subsp. nov. . . . 247
Remopleurella burmeisteri (Bancroft) gen. nov. . . . 250
Family Thysanopeltidae Hawle & Corda 251
Eobronteus ? sp. 251
II. References 251

Family Calymenidae Burmeister, 1843

Genus ***FLEXICALYMENE*** Shirley, 1936

Type species. *Calymene Blumenbachii* var. *Caractaci* Salter, 1865 by original designation of Shirley (1936 : 395).

Flexicalymene acantha Bancroft

(Pl. 37, figs. 1, 3–6, 14)

1949. *Flexicalymene acantha* Bancroft, p. 305, pl. 11, figs. 29, 30.
1958. *Flexicalymene acantha* Bancroft : Dean, p. 219.

Bancroft's original description was founded on two specimens, the holotype cranidium and a paratype pygidium, both probably immature. A few large topotype cranidia have been collected and these show slight differences from the holotype. The anterior border is somewhat shorter proportionately and a little less steeply upturned, the frontal glabellar lobe is more rounded, and there is a well-defined break in the glabellar outline, so that the latter narrows sharply, immediately in front of the second glabellar lobes. Where the external impression of the test is available it is seen to be practically smooth, with only occasional traces of tubercles, contrasting markedly with the almost prickly appearance of immature specimens. One specimen has been found with thorax complete (Pl. 37, fig. 14). There are thirteen segments of normal calymenid type and the surface of the axial rings and pleurae, excluding furrows, is ornamented with small tubercles ; again, the specimen represents an immature individual. The pygidium figured by Bancroft (1949, pl. 11, fig. 30) has the axis distorted by crushing so that it appears too narrow ; normally it occupies frontally about one-third of the maximum breadth. There are six axial rings, of which the sixth is poorly defined, and five pairs of furrowed pleural ribs, not six as stated by Bancroft (1949 : 305). No well-preserved pygidium of *F. acantha* has yet been found in association with the cephalon of the species, therefore some doubt must exist as to the true identity of the paratype pygidium, as another calymenid, *Gravicalymene praecox* (Bancroft), occurs in the same strata.

Horizon and Localities. In the Costonian Stage of the Coston district, near Aston-on-Clun, and at Brokenstones, near Horderley, there occur numerous calymenids which are close to Bancroft's species, and some are figured here as *Flexicaly-*

mene cf. *acantha* (Pl. 37, figs. 7, 10, 13). Such differences as exist, for example, degree of inclination of the anterior border, straightening of the normally convex margins of the glabella, and variation in the shape of the frontal glabellar lobe, could well be the result of mechanical deformation and it is not proposed to regard them as distinct from *F. acantha*. The earliest known, uncommon occurrences are in the middle Costonian of Coston but specimens are moderately abundant in the succeeding upper Costonian.

The type locality is the old cartway section near the south end of Smeathen Wood, Horderley, 250 yards west-south-west of Wood House, where the species occurs in small numbers in the lowest Smeathen Wood Beds, Harnagian Stage, *Reuscholithus reuschi* Zone. *Flexicalymene acantha* has been found neither at higher horizons, nor outside the southern part of the Caradoc district. In the northern part of the district, however, *Flexicalymene* (*s.s.*) is believed to occur in the topmost Costonian Stage, near Cressage, but the available specimens are too fragmentary to ascertain whether another species is represented ; furthermore the dominant form in the Cressage strata is *Flexicalymene* (*Reacalymene*) *pusulosa* (Shirley).

HOLOTYPE. BM. In. 42091 (Pl. 37, fig. 3).

PARATYPE. BM. In. 49592 (Pl. 37, fig. 4).

DISCUSSION. For convenience the discussion of the species of *Flexicalymene* (*s.s.*) has been placed after the description of *F. cobboldi*.

Flexicalymene planimarginata (Reed)

(Pl. 37, fig. 15)

1906. *Calymene planimarginata* Reed, p. 137, pl. 17, fig. 15.
1960. *Flexicalymene planimarginata* (Reed), Whittard, p. 158. Includes full synonymy of the species.

A few pygidia have been collected from the Lower Longvillian Substage south of the Onny Valley, and the most complete is figured here.

Preserved as an internal mould it shows all the features mentioned by Harper (1947 : 167) in his re-description of the species, though comparison with the somewhat distorted topotype figured by him (Pl. 6, fig. 12) is difficult. The Shropshire specimen now illustrated is from the *Dalmanella horderleyensis* Zone, that is to say only slightly earlier than the horizon yielding the type-specimen at Ynys Galed, Caernarvonshire. Whittard (1960 : 158) has recently found the same species in west Shropshire, where it occurs earlier, in the Soudleyan Stage.

Flexicalymene caractaci (Salter)

(Pl. 38, figs. 2, 4–6, 8, 11, 12)

1865*a*. *Calymene Blumenbachii* var. *Caractaci* Salter, p. 96, pl. 9, fig. 3.
1931. *Calymene caractaci* Salter : Shirley, p. 25, pl. 2, figs. 4–6.
1936. *Flexicalymene caractaci* (Salter) Shirley, p. 395, figs. 1, 2.
1949. *Flexicalymene trigonoceps* Bancroft, p. 306, pl. 11, figs. 31, 32.

Specimens of this well-known species are common in the Caradoc Series of south Shropshire, but records of its existence outside the district are suspect and its true distribution in the Anglo-Welsh area is by no means well known, though its apparent absence is likely to result from the lack of the appropriate strata over much of Wales.

Flexicalymene caractaci was re-described by Shirley (1931 : 25) using Salter's type-material, which comprises a large slab of highly fossiliferous, decalcified sandstone. The lithology is typically that of the Upper Cheney Longville Flags, of Marshbrookian age, and this is confirmed by the fauna which includes, in addition to *F. caractaci*, abundant *Dalmanella wattsi* (Bancroft) and *Broeggerolithus transiens* (Bancroft). The specimen illustrated by Shirley (1931, pl. 2, fig. 4) and refigured here (Pl. 2, fig. 6) is now chosen as lectotype as it corresponds best with Salter's original illustration. Little need be added to Shirley's detailed description, but it may be noted that the anterior border is somewhat variable in length, and that its angle of inclination may be dependent on the state of preservation. For this reason Bancroft's *Flexicalymene trigonoceps*, said by him to have an anterior border less steeply inclined than that of *F. caractaci*, is now considered to fall within the limits of variation of the latter species. The earliest undoubted occurrences in south Shropshire are in the lowest Marshbrookian Stage, the *Dalmanella wattsi* Zone, at which level it is to be found in abundance at several localities, but fragmentary evidence from the *Kjaerina typa* Zone of the Upper Longvillian Substage in the Onny Valley suggests that it may have appeared there somewhat earlier. *F. caractaci* is generally found wherever the strata of the *Dalmanella unguis* Zone crop out ; in the topmost third of the Marshbrookian, the *Onniella reuschi* Zone, the species is noticeably less common, and as yet it has been found neither in the overlying Actonian Stage nor co-existing with species of *Onnicalymene*.

LECTOTYPE. GSM. 47698 (Pl. 38, fig. 6).

Flexicalymene cobboldi sp. nov.

(Pl. 38, figs. 1, 3)

DIAGNOSIS. *Flexicalymene* (*s.s.*) with relatively short, well-rounded glabella. Anterior border long, steeply inclined frontally, and convex forwards in plan. Eyes situated opposite second glabellar lobes and furrows.

DESCRIPTION. The cranidium is moderately convex both longitudinally and transversely, with the maximum breadth twice the median length. The glabella is plump and short, about as broad as long, its outline subparabolic. The frontal glabellar lobe is small and short, only about one-seventh of the glabellar length, broadly rounded frontally and defined posteriorly by short (*tr.*), shallow, first glabellar furrows slightly divergent posteriorly, parallel to the small, ovoid, first glabellar lobes. The second glabellar lobes are larger, subcircular in plan, about half the length (*exsag.*) of the third lobes, which are of the " cat's ear " form described by Shirley (1931 : 20, 26). The second glabellar furrows are deep, widening (*exsag.*) adaxially and showing traces of branching. The third glabellar furrows are somewhat wider, deeper and distinctly bifid, the anterior branches being the shorter, continuing across the bases of the second lobes, whilst the posterior branches end opposite the mid-points of the third lobes, though there is a suggestion of their continuation as shallow grooves across the neck-like structures connecting the lobes to the median glabellar lobe. The unfurrowed median lobe of the glabella is broad, with almost no development of what Shirley (1936 : 386) termed intermediate lobes. The axial furrows are broad, curved, gently convergent forwards, shallowing slightly opposite the second glabellar lobes. The anterior border is long, well rounded in plan, and of scoop-like form, steeply inclined forwards. The palpebral lobes, incompletely known, are sited in line with the second glabellar lobes and furrows. The remainder of the cranidium contains no diagnostic features, and is identical with that of *Flexicalymene caractaci*, a closely-related species. The librigenae, hypostoma, thorax and pygidium are not known.

HORIZONS AND LOCALITIES. The holotype is from the Upper Longvillian Substage, *Kjaerina bipartita* Zone, by the south-eastern side of the road between Horderley and Marshbrook, 420 yards north-east of the building known as Crosspipes. At this point the specimen was collected from grey-green mudstones which are interbedded with limestone lenses containing *Heterorthis alternata* (J. de C. Sowerby), the whole being grouped together as the " *Alternata* Limestone ". The paratype, the only other specimen known, is from the Marshbrookian Stage, *Dalmanella unguis* Zone, at Marsh Wood Quarry, half-a-mile south of Marshbrook Station. The fossil band containing this specimen did not yield any other specimens of *Flexicalymene*, though *F. caractaci* has been found in abundance at other levels in the same quarry.

HOLOTYPE. BM. In. 55448 (Pl. 38, fig. 3).

PARATYPE. BM. In. 50762 (Pl. 38, fig. 1).

DISCUSSION. The stratigraphically earliest known species of *Flexicalymene* (*s.s.*) in south Shropshire is *F. acantha*, the glabellar outline of which, narrowing sharply in front of the second glabellar furrows, is remarkably suggestive of that found in *Flexicalymene cambrensis* (Salter, 1865), a Llandeilo species which has been refigured by Shirley (1931 : 20, pl. 1, figs. 11–15), and the two forms may be related. However, the anterior border of *F. acantha* is noticeably the shorter of the two, whilst the palpebral lobes of *F. cambrensis* are situated farther forwards than in the Harnagian species.

In the collections of the Geological Survey & Museum there are two specimens labelled " *Calymene fatua* ", a manuscript name proposed by Salter but never published. One of these specimens, numbered 19603, is a typical, though distorted, cranidium of *Flexicalymene acantha* from " Horderley ". The other is an unidentifiable, damaged cranidium, 19604, apparently a *Flexicalymene* or *Reacalymene*, alleged to be from " Gretton ". This locality is probably incorrect, as only strata of Marshbrookian or Actonian age crop out in the vicinity of Gretton village, whereas the matrix of the specimen suggests rather a derivation from the Chatwall Flags, of Soudleyan age.

Calymene incerta Barrande (1852 : 568, pl. 19, figs. 30, 36) was stated to occur at a number of localities in Bohemia, and the illustrated specimens show some variation in the proportions of the glabella, so that more than one form may be present. The species may be referred to *Flexicalymene* (*s.s.*), and specimens in the Barrande Collection at the British Museum (Nat. Hist.) from Zahoržan, one of the localities listed in the original description, show the anterior border to be relatively short, suggesting a comparison with species such as *F. acantha* and *F. planimarginata*, rather than with *F. caractaci* and *F. declinata* (see later). In general, *Flexicalymene incerta* appears to be larger than any of the Anglo-Welsh species, with a glabellar outline much broader frontally than either *F. acantha* or *F. planimarginata*, although one of the specimens figured by Barrande (1852, pl. 19, fig. 32 only) has a glabella reminiscent of *F. acantha*. According to Barrande (1852 : 569), *F. incerta* is accompanied by *Trinucleus ornatus* (now *Onnia ornata* Sternberg sp.) and *Calymene pulchra* (now *Pharostoma pulchrum* Beyrich sp.), and is unlikely to be later than Caradoc in age.

The species to which *Flexicalymene caractaci* bears, perhaps, the strongest resemblance is *F. declinata* (Hawle & Corda), described originally from the Ordovician of Beraun (Hawle & Corda, 1847 : 87), but figured first by Barrande (1852 : 570, pl. 43, figs. 53–58). The glabellar outline is closely similar in both species, but the eyes of *F. declinata* are situated farther forwards, opposite the first glabellar lobes, whilst the outline of the anterior border is less well-rounded than that of *F. caractaci*. According to Barrande (1852 : 572), *F. declinata* is found in company with *Remopleurides radians* (now *Amphitryon radians* Barrande sp.) and *Trinucleus Bucklandi* (now *Tretaspis granulata* Wahlenberg sp.), species which suggest an Ashgill age.

Flexicalymene caractaci and *F. cobboldi* may readily be separated from the earlier *F. acantha* and *F. planimarginata* by their longer anterior border as well as by the glabellar outline, whilst the glabella of *F. caractaci* is longer than that of *F. cobboldi*. The short glabella of the last-named species is not unlike that of *Flexicalymene brevicapitata* Portlock sp. (Shirley, 1931 : 28, pl. 2, figs. 9, 10) from, probably, the Killey Bridge Beds of Tyrone, but the latter lacks definite first glabellar lobes and the eyes are situated slightly farther forwards than in the Shropshire trilobite.

Subgenus ***REACALYMENE*** Shirley, 1936

TYPE SPECIES. *Reacalymene limba* by original designation of Shirley (1936 : 395).

Flexicalymene (Reacalymene) pusulosa (Shirley)

(Pl. 37, figs. 9, 11, 12)

1936. *Reacalymene pusulosa* Shirley, p. 407, pl. 29, figs. 9, 10.
1958. *Reacalymene pusulosa* Shirley : Dean, pp. 198, 218.
1962. *Flexicalymene (Reacalymene) pusulosa* (Shirley) Dean, p. 113.

Numerous specimens corresponding in all details with Shirley's original description of the species have been found in the topmost subdivision, the *Harknessella subquadrata* Zone or Limestone, of the Costonian Stage in the Harnage District, where it occurs at several localities. In the southern part of the Caradoc District, several miles south of Harnage, the Costonian strata become less calcareous and more arenaceous than at Harnage and have not yielded material which can satisfactorily be assigned to *F. (R.) pusulosa*. The evidence suggests that the species has a somewhat restricted horizontal as well as vertical distribution, and that farther south it is replaced by *Flexicalymene acantha* Bancroft. Although Shirley stated that the pygidium of *F. (R.) pusulosa* possesses four pleural ribs and six axial rings, further collecting shows that some specimens may have five pleural ribs and traces of a seventh axial ring.

HOLOTYPE. This specimen, a cranidium, was originally part of the E. S. Cobbold collection, housed in the Shrewsbury Museum, but has since been transferred to the British Museum (Nat. Hist.) where it is numbered In. 50780 (Pl. 37, figs. 9, 11).

LOCALITIES. The holotype is from the disused quarry near the eastern end of Black Dick's Coppice, Evenwood, whilst the other figured specimen is from the small quarry in the north-western part of Round Nursery, south of Harnage Grange.

Flexicalymene (Reacalymene) cf. ***limba*** (Shirley)

(Pl. 37, fig. 16)

1936. *Reacalymene limba* Shirley, p. 409, pl. 29, figs. 11–13.
1960*a*. ? *Reacalymene pusulosa* Shirley : Dean, p. 167.
1961. *Reacalymene limba* Shirley : Whittard, pl. 22, fig. 5.

An incomplete cranidium preserved as an internal mould resembles the species described by Shirley in all essentials, as far as can be ascertained. Shirley distinguished *Reacalymene limba* from *R. pusulosa* by the former's possession of a less convex glabella and longer " preglabellar field " (=anterior border). He also pointed out that *R. limba* lacked the so-called " supplementary " furrows on the glabella just behind the hypostomal pits, and such furrows appear to be absent from the present specimen. In addition it may be stated that the sides of the glabella are more convergent forwards in *F.* (*R.*) *limba* than in *F.* (*R.*) *pusulosa*, resulting in a distinctive, triangular appearance.

HORIZON AND LOCALITY. The so-called " *Glyptocrinus* Flags ", Soudleyan Stage, probably *Broeggerolithus broeggeri* Zone, at the small, disused, road-side quarry 150 yards north-east of Chatwall Farm, Chatwall. Shirley (1936 : 409) believed, though with reservations, that the holotype of *F.* (*R.*) *limba* originated from the Rhiwlas Limestone, Ashgill Series, of the Bala District, but recently Whittard (1960 : 158) has recorded the species from the Shelve Inlier, at the same horizon as the present specimen. Despite extensive collecting the species has not been found at any other horizon in south Shropshire, and Shirley's record (1936 : 408) of rare *Reacalymene pusulosa* in the *Glyptocrinus* Flags may refer, in fact, to forms such as that now figured.

Flexicalymene (Reacalymene) horderleyensis sp. nov.

(Pl. 37, figs. 2, 8 ; Pl. 40, figs. 7, 8)

?1947. *Flexicalymene* sp. nov., Harper, p. 168, pl. 6, fig. 10.
1958. *Reacalymene* sp. nov., Dean, p. 221.

DIAGNOSIS. Species of *Reacalymene* characterized by subtriangular glabella with short frontal lobe, and long, steeply inclined anterior border with low, transverse ridge.

DESCRIPTION. The species is known, so far, from only three isolated cranidia, two of them external moulds, the other an internal mould. The glabella is slightly longer than broad, roughly subtriangular in plan with almost straight lateral margins converging forwards at about 35 degrees to a short, broadly rounded, frontal glabellar lobe. There are three pairs of lateral glabellar lobes, those of the basal pair the largest, broadly oval in plan, slightly divergent forwards, and bluntly pointed anterolaterally. The second glabellar lobes are about half the size of the third pair, oval in plan, broadly divergent forwards and parallel to the lobes of the first pair, which are short and subrectangular. The first glabellar lobes are separated from the frontal glabellar lobe by short, shallow, first glabellar furrows which are parallel to the long axes of the first lobes. The second glabellar furrows run parallel to those of the first pair, but are deeper, bifurcating slightly so that the posterior branch is the longer. The third glabellar furrows are more markedly bifid, the anterior branches short, curving around the second glabellar lobes, the posterior branches running backwards and ending just short of the occipital furrow ; the two branches are separated by a small, convex lobe-like swelling. All the glabellar lobes and furrows end in-line adaxially, leaving a median body which is roughly parallel sided and occupies a little less than half the breadth of the glabella. The anterior border is long, convex forwards medially, slightly ridged posteriorly on the external mould (Pl. 37, fig. 2), though apparently smooth on the internal mould (Pl. 40, fig. 8) ; it is separated from the preglabellar field by a shallow, anterior border furrow. What may be described as the preglabellar field is short (*sag.*), gently inclined forwards, expanding laterally, truncated by the well-impressed preglabellar furrow which is continuous with the deep, narrow axial furrows. The occipital furrow is shallow and transversely straight medially, deepening laterally, at the same time becoming convex backwards as it circumscribes the third glabellar lobes. Similarly, the occipital ring is transversely straight and of uniform length (*sag.*) medially, shortening laterally where it forms a pair of poorly defined occipital lobes, strongly divergent forwards, and indistinctly separated from the posterolateral parts of the fixigenae. The posterior border furrow is broad (*exsag.*), straight, of uniform and moderate depth, delimiting a posterior border which is narrow (*exsag.*) adaxially, broadening towards the genal angles. The anterior portions of the fixigenae are of uniform breadth, almost half that of the frontal glabellar lobe, and parallel-sided as far as the palpebral lobes, whilst the posterior portions are steeply declined. The palpebral lobes are laterally convex in plan, situated opposite the second glabellar lobes, with poorly-defined eye-ridges running from the anterior ends of the lobes to end at the axial furrows opposite the first glabellar lobes. The facial suture is of characteristic calymenid type, the anterior branches converging gently from the eyes to cut the anterior margin at points which lie longitudinally between the palpebral lobes and the axial furrows, whilst the posterior branches curve backwards from the eyes, at first gently and then more strongly to the genal angles. The surface of the test is poorly known from only two external moulds, but appears to be finely granulate.

The librigenae, hypostoma, thorax and pygidium are not known.

HORIZON AND LOCALITIES. The holotype and one paratype are from the Lower Longvillian Substage, zone of *Dalmanella indica* and *D. lepta,* at the outcrop inside the south-eastern corner of Rookery Wood, south-east of Horderley. The remaining paratype is from a similar horizon at the small disused quarry just west of the western end of Rookery Wood. Fragmentary evidence of what may prove to be the same species has been obtained from the underlying *Dalmanella horderleyensis* Zone at Long Lane Quarry, three-quarters of a mile north-west of Craven Arms.

HOLOTYPE. BM. In. 50656 (Pl. 37, figs. 2, 8).

PARATYPES. BM. In. 49559, BM. In. 52103 (Pl. 40, figs. 7, 8).

DISCUSSION. *Flexicalymene* (*Reacalymene*) *horderleyensis* bears a general resemblance to *F.* (*R.*) *limba*, from which it is distinguished by its longer, more steeply upturned anterior border, and shorter frontal glabellar lobe. In the Welsh Borders the known species of *Reacalymene*, namely *pusulosa*, *limba* and *horderleyensis*, derive successively from Costonian, Soudleyan and Lower Longvillian strata, and form a morphological series, with a progressive increase in the length of the anterior border, and in the degree of convergence of the axial furrows.

The internal mould of a calymenid cranidium described and figured by Harper (1947 : 168, pl. 6, fig. 10) as *Flexicalymene* sp., from the Lower Longvillian of Ynys Galed, North Wales, has apparently undergone some tectonic deformation, but nevertheless bears a general resemblance to *F.* (*R.*) *horderleyensis*, particularly in the glabellar outline and long anterior border (compare Pl. 4, fig. 7). The two may be synonymous, but a final decision must await the collection of additional Welsh material.

Calymene croneisi Roy, 1941, from the Ordovician, possibly Trenton, of Baffin Island, was recently redescribed by Whittington (*in* Miller *et al.*, 1954 : 147, pl. 62, figs. 13–15) and assigned to *Flexicalymene*, though he noted that the anterior border is ridged as in *Reacalymene*. *Flexicalymene* (*Reacalymene*) *croneisi* bears a general resemblance to the Anglo-Welsh species, but is particularly distinguished by the forward position of the palpebral lobes, opposite the second glabellar furrows and part of the first glabellar lobes. The anterior border of the North American form, like that of *F.* (*R.*) *pusulosa*, is relatively short and transversely straight, which feature easily separates it from *F.* (*R.*) *horderleyensis*, whilst the glabellar outline is narrower than that of *F.* (*R.*) *pusulosa*.

Genus ***ONNICALYMENE*** Dean, 1962

TYPE SPECIES. *Flexicalymene onniensis* Shirley, 1936 by original designation of Dean (1962 : 112).

Onnicalymene onniensis (Shirley)

(Pl. 39, figs. 2, 10, 11; Pl. 40, fig. 9)

1865. *Calymene brevicapitata* Portlock, Salter, pl. 9, fig. 7.
1936. *Flexicalymene onniensis* Shirley, p. 405, pl. 29, figs. 5–7.
1949. *Flexicalymene onniensis* Shirley : Bancroft, p. 308, pl. 11, figs. 36, 37.
1958. *Flexicalymene onniensis* Shirley : Dean, p. 224.
1959. *Flexicalymene onniensis* Shirley : Dean, pp. 200, 207.
1959. *Flexicalymene* aff. *onniensis* Shirley : Dean, pp. 202, 208.
1962. *Onnicalymene onniensis* (Shirley) Dean, p. 115, pl. 13, figs. 7; pl. 14, figs. 1, 2, 7, 10.

The species was first described by Shirley (1936) from the *Onnia gracilis* Zone of the Onnian Stage in the River Onny Valley. The most likely site of the type-locality is the prominent, ridge-like outcrop in the river-bed about 100 yards of its junction with the stream of Batch Gutter, and at this point *O. onniensis* occurs abundantly with the zonal trinucleid. There is ample evidence that the species ranges upwards into and through the succeeding *Onnia superba* Zone, but evidence of its earlier occurrence is tenuous. Possible fragments have been found in the *Onnia ? cobboldi* Zone of the Onny Valley, but all the identifiable specimens of *Onnicalymene* so far collected from the underlying Actonian Stage have proved to belong to other species. Outside Shropshire *O. onniensis* occurs at Welshpool, in the *Onnia gracilis* Zone, and in the Dufton Shales of the Cross Fell Inlier, where it has an extended vertical range upwards into the Pusgillian Stage (Dean, 1962 : 115).

HOLOTYPE. GSM. RR 1940 (Pl. 39, figs. 10, 11).

Onnicalymene laticeps (Bancroft)

(Pl. 38, figs. 7, 10, 14, 15)

1949. *Flexicalymene laticeps* Bancroft, p. 307, pl. 11, figs. 33, 33*a*.
1958. *Flexicalymene laticeps* Bancroft : Dean, p. 224.
1962. *Onnicalymene laticeps* (Bancroft) Dean, p. 115, pl. 14, figs. 5, 6.

This small, easily-recognized species of *Onnicalymene* has been found at several localities in Shropshire, in both mudstones and sandstones of the Actonian Stage. *O. laticeps* has been recorded also in the Cross Fell Inlier (Dean, 1962 : 115), and may prove to be of stratigraphical value. It is readily separated from other species of the genus by its short, well-rounded glabella.

HOLOTYPE. BM. In. 42103 (Pl. 38, fig. 7).

Onnicalymene salteri (Bancroft)

(Pl. 38, figs. 9, 13)

1949. *Flexicalymene salteri* Bancroft, p. 306, pl. 11, figs. 34, 35.
1958. *Flexicalymene salteri* Bancroft : Dean, p. 224.
1962. *Onnicalymene salteri* (Bancroft) Dean, p. 113.

This species was founded on two cranidia, both of Actonian age, one, the holotype, from the northern end of the small wood west of Rose Villa, Marshbrook, the other from the locality known as Jack Slither, in the south bank of the River Onny, 45 yards west of its junction with the stream of Batch Gutter. Both specimens occur in grey, calcareous mudstones, a lithology which contains most of the known specimens, though a few have been collected from limestone bands of the Actonian in the vicinity of Jack Slither. *Onnicalymene salteri* has not yet been found in the arenaceous facies of the Actonian, such as is found at and near Acton Scott and Cardington, nor is it known to occur at any horizon other than the Actonian. It is subordinate in numbers to the contemporaneous *Onnicalymene laticeps* (Bancroft), and has not been recorded outside Shropshire.

HOLOTYPE. BM. In. 42100 (Pl. 38, fig. 9).

PARATYPE. BM. In. 42099.

Genus ***GRAVICALYMENE*** Shirley, 1936

TYPE SPECIES. *Gravicalymene convolva* by original designation of Shirley (1936 : 395).

Gravicalymene praecox (Bancroft)

(Pl. 39, figs. 1, 3, 9, 12–14)

1949. *Diacalymene praecox* Bancroft, p. 308, pl. 11, figs. 28, 28*a*.
1958. *Diacalymene ? praecox* Bancroft : Dean, p. 219.
1962. *Gravicalymene praecox* (Bancroft) Dean p. 113.

The holotype of *Gravicalymene praecox*, like the lectotype of *Flexicalymene acantha*, from the same locality and horizon, is a small immature cranidium (Pl. 39, figs. 13, 14). The photograph used by Bancroft (1949, pl. 11, fig. 28) to illustrate the species was taken obliquely from the right-hand side of the specimen ; consequently, what might appear to be a constriction of the right axial furrow is really an illusory effect produced by the convexity of the right fixigena in line with the axial furrow. In fact, the axial furrows of the holotype show no lateral constriction, and the species cannot, therefore, be placed in *Diacalymene*. Both *Diacalymene* and *Gravicalymene* have recently been discussed (Dean, 1962) and it has been shown that the earlier usage of the terms " ridged " and " roll-like " with regard to the form of the anterior border is unsatisfactory as a basis for generic differentiation, but that the form of the axial furrows is more reliable. On these grounds, therefore, *Diacalymene praecox* must be transferred to *Gravicalymene*. During recent collecting, additional topotype material has been obtained which apparently represents mature adult specimens of the species (Pl. 39, figs. 1, 3, 9, 12). All are internal moulds of incomplete cranidia, and they show little change from the holotype, though the granulation of the test found on the latter specimen seems to have disappeared when the adult stage was attained.

A cranidium from the Actonian Stage at Gretton, GSM. 19588, constituted one of the syntypes of Salter's (1865*a*, pl. 9, fig. 4 only) *Calymene Blumenbachii* var. *Caractaci* whilst another cranidium from the same locality was assigned to the same species by La Touche (1884, pl. 3, fig. 61). These stratigraphically later forms of *Gravicalymene* are undoubtedly extremely close to *G. praecox*, with which species they are compared here, though identification cannot be certain in the absence of complete, uncrushed, adult cranidia of the Harnagian species. The thorax, of characteristic calymenid form, with thirteen thoracic segments, was found in juxtaposition to both cranidium and pygidium in strata of Onnian age (Pl. 39, figs. 4, 5, 8). The pygidium is strongly convex both longitudinally and transversely, the dorsal surface of the axis being gently convex, steeply declined posteriorly. The outline of the pygidium, when viewed from above with the axis horizontal, is broadly semi-elliptical frontally, the posterolateral margins being straight, strongly divergent forwards as far as the line of maximum breadth, opposite the midpoint of the pygidium. The axis is broadest frontally, where it is equal to one-third the maximum pygidial breadth, but narrows a little backwards, and stops short of the the tip of pygidium. Excluding the articulating half-ring, there are seven well-defined axial rings, and the axial furrows are straight, slightly convergent backwards where they are continued so as to circumscribe the terminal piece, which is of moderate size and a little less than one-quarter the length of the axis. The pleural lobes are strongly arched-down laterally, with six pairs of well-defined, evenly curved ,pleural ribs, and a seventh, less well-defined pair fused together to form a low, postaxial ridge. Each pleural rib is divided into two bands of almost equal breadth (*exsag.*) by a narrow, shallow, interpleural furrow which cuts the posterior margin of the rib at its intersection with the axial furrow.

HORIZONS AND LOCALITIES. *Gravicalymene praecox* was first described from the Smeathen Wood Beds, Harnagian Stage, *Reuscholithus reuschi* Zone, exposed in the old cartway at the southern end of Smeathen Wood, Horderley. What is probably the same form has been found, rarely, at the corresponding horizon in the north bank of Coundmoor Brook, about 1,295 yards south-west of Harnage Farm, Harnage. As noted earlier, specimens referred to *Gravicalymene* cf. *praecox* have been collected from both the Actonian and Onnian Stages. Actonian localities include the old quarry 210 yards east of Acton Scott church, and the now unavailable quarry at Quarry Field, Gretton, near Cardington (see Pl. 39, fig. 7). The only Onnian locality at which *G.* cf. *praecox* has been found is in rocks of the *Onnia gracilis* Zone, exposed in the north bank of the River Onny 100 yards east of its junction with Batch Gutter. These occurrences, at widely separated horizons within the Caradoc Series, are particularly interesting as no evidence of *Gravicalymene* has been found in the intervening strata. It may be noted, however, that in each case the appearance of the genus is associated with an influx of new faunal elements, and this, in turn, may be correlated with a marine transgression which affected much of the Anglo-Welsh area. The lower of these is the *Nemagraptus gracilis* Transgression, which continued into the overlying *Diplograptus multidens* Zone ; the higher transgression is that occurring high in the *Dicranograptus clingani* Zone, and perhaps also in the *Pleurograptus linearis* Zone, which gave rise to dark shales and mudstones, including the Nod Glas, in North Wales.

HOLOTYPE. BM. In. 42090 (Pl. 39, figs. 13, 14).

DISCUSSION. Of the other recorded species of *Gravicalymene* in the British Ordovician, *G. jugifera* Dean (1962, pl. 13, figs. 9, 11 ; pl. 14, figs. 3, 4, 8, 9) from the Pusgillian Stage of the Cross Fell Inlier differs from *G. praecox* in having proportionately smaller basal glabellar lobes, a less quadrate frontal glabellar lobe, and an anterior border which is separated from the glabella by a broader (*sag.*), more conspicuous furrow. *Gravicalymene convolva* Shirley (1936 : 409, pl. 29, figs. 16–18) is a relatively large species which may be distinguished from *G. praecox* by its broader glabellar outline, with slightly smaller basal glabellar lobes and conspicuously shorter frontal glabellar lobe.

The trilobite figured by Størmer (1945, pl. 2, figs. 6–8) as *Reacalymene holtedahli* from Stage 4cα of Hadeland, Norway (an horizon approximately equivalent to the Pusgillian Stage) is probably best placed in *Gravicalymene* or *Diacalymene*. It may be distinguished from *G. praecox* by its narrower glabellar outline, smaller glabellar lobes, and shorter frontal glabellar lobe. One of Størmer's syntypes appears to show the second glabellar lobes in contact with the fixigenae, but, judging from the distortion of the specimen, this may well be due to mechanical causes. The pygidium of the Norwegian form has fewer axial rings and pleural ribs than that described in the present paper as *Gravicalymene* cf. *praecox*.

It was claimed by Bancroft (1949 : 309) that what he called *Diacalymene praecox* was important in anticipating a form of Ashgill age, probably *D. marginata* Shirley, judging from his text. Now that *D. praecox* can be assigned to *Gravicalymene*, such a claim is without foundation, and the species probably represents nothing more than one member of a long-ranging genus. The trilobite figured by Shirley (1931, pl. 2, fig. 11) as *Calymene quadrata* ? King, from the Llandeilo Flags of South Wales, is too badly preserved for certain identification, but bears some resemblance to *Gravicalymene*, and suggests that the genus may have appeared in the Anglo-Welsh area before the beginning of Caradoc times. *Gravicalymene* had a remarkably long stratigraphical range, and has been recorded as late as the Devonian from New Zealand (Shirley, 1938).

Gravicalymene inflata sp. nov.

(Pl. 39, fig. 6)

1958. *Gravicalymene* sp. nov., Dean, p. 224.

DIAGNOSIS. Species of *Gravicalymene* with short (*sag.*), transversely straight, anterior border. Frontal glabellar lobe moderately long, markedly quadrate in plan. Fixigenae strongly convex, almost as anteriorly broad as frontal glabellar lobe. Palpebral lobes sited opposite second glabellar furrows and anterior half of second glabellar lobes.

DESCRIPTION. The only available specimen is an incomplete cranidium, lacking the posterior halves of the fixigenae, but with the test preserved. The median length is about 15 mm., and the frontal breadth, as measured across the anterior portion of the fixigenae, is 17 mm.

The glabella is slightly longer than broad, approximately in the ratio 6 : 5, but the proportions are somewhat distorted by crushing of the basal glabellar lobes, which constitute the line of greatest breadth. The frontal glabellar lobe is markedly rectangular in outline, its breadth more than twice the length. There are three pairs of glabellar lobes, those of the third pair being the largest, becoming subangular anterolaterally. The second glabellar lobes are considerably smaller than those of the third pair, oval in shape with their long axes gently divergent forwards. The third lobes are of subcircular form, about half the size of the second lobes ; they are defined anteriorly by short (*tr.*), transversely straight, first glabellar furrows which widen (*exsag.*) slightly adaxially. The second glabellar furrows are at first transversely straight from the axial furrows, but quickly bifurcate, the anterior branch so formed being short, and the posterior branch longer, extending backwards until opposite the mid-points of the second glabellar lobes. The third glabellar furrows extend backwards from the axial furrows for almost the length (*tr.*) of the second glabellar lobes before bifurcating, the shorter, anterior branch then running forwards towards, but not meeting, the posterior branch of the second glabellar furrows. The posterior branches of the third glabellar furrows are longer (*exsag.*), and appear to end opposite the middle of the third glabellar lobes but, as the latter are partly crushed, this feature cannot be properly examined. The glabellar lobes are thus connected to the median glabellar lobe by constricted, neck-like structures which, as far as can be seen, are slightly depressed dorsally, though there is no development of definite furrows. The axial furrows are narrow, uniformly deep, almost parallel frontally as far as the second glabellar furrows ; they then diverge slightly as far as the third glabellar furrows, beyond which they diverge more strongly, curving round the abaxial margins of the basal glabellar lobes to intersect the occipital furrow. The anterior border is conspicuously short (*sag.*), one-seventh of the median length of the glabella, becoming even shorter abaxially, beyond the axial furrows ; the anterior margin is transversely straight, as is the posterior margin opposite the frontal glabellar lobe, though there is a slight lengthening (*exsag.*) opposite the axial furrows. The flattened upper surface of the anterior border is inclined forwards at only a small angle to the dorsal surface of the glabella, that is to say, it would be approximately horizontal when the cranidium was in its, presumably, normal position. The anterior border and frontal glabellar lobe are separated by a deep, narrow (*sag.*), transversely straight furrow which curves slightly forwards abaxially beyond the axial furrows to separate the anterior border from the fixigenae. The occipital ring is relatively long (*sag.*), in length about one-sixth that of the glabella, parallel-sided medially, but shortening (*exsag.*) abaxially to accommodate the projecting posterior margins of the basal glabellar lobes, and forming a pair of poorly-defined occipital lobes. The occipital furrow is both shallow and transversely straight medially, but deepens distally, becoming convex backwards around the basal glabellar lobes. The pleuroccipital furrow, posterolateral portions of the fixigenae and the posterior branches of the facial suture, are not preserved. The palpebral lobes are of moderate size, inclined gently towards the lateral margins, and extending from opposite the second glabellar furrows to opposite the third glabellar furrows. The fixigenae are strongly convex both transversely and longitudinally, standing highest opposite the second glabellar lobes. They are parallel-sided frontally, the anterior branches of the facial suture running straight forwards from the eyes, and there is a pair of poorly defined eye-ridges extending slightly forwards adaxially from the anterior ends of the palpebral lobes and ending at the axial furrows opposite the first glabellar lobes. The surface of the test, excluding the furrows, all of which are smooth, is covered with fine, closely-set granules, generally of uniform size ; slightly larger granules occur sporadically, and uncommonly, over the surface of the glabella and fixigenae, becoming more common on the anterior border.

The hypostoma, thorax and pygidium are not known.

HORIZON AND LOCALITY. The only known specimen is from the Onnian Stage, *Onnia gracilis* Zone, in the north bank of the River Onny, 100 yards east of its junction with Batch Gutter.

HOLOTYPE. BM. In. 50653 (Pl. 39, fig. 6).

DISCUSSION. This rare form is distinctive, and may easily be separated from all other known species of the genus, for example *G. praecox*, by the unusually short (*sag.*), straight anterior border, and by the large, inflated fixigenae, which are much broader than those of other forms. In addition, the palpebral lobes are situated farther forwards than those of *G. praecox*.

Family ASAPHIDAE Burmeister, 1843

Subfamily ASAPHINAE Burmeister, 1843

Recently *Parabasilicus* was placed by Jaanusson (*in* Moore, 1959 : 342) in the subfamily Isotelinae, whilst *Basilicus* was assigned to the Asaphinae. The affinities of *Parabasilicus* appear to lie with *Basilicus* rather than with the other genera of the Isotelinae, and accordingly the genus is here transferred to the Asaphinae.

Genus ***PARABASILICUS*** Kobayashi, 1934

TYPE SPECIES. *Parabasilicus typicalis* by original designation of Kobayashi (1934 : 475).

Parabasilicus powisi (Murchison)

(Pl. 40, figs. 1, 3–5 ; Pl. 41, figs. 1, 2 ; Pl. 42, fig. 9)

1839. *Asaphus powisi* Murchison, p. 661, pl. 23, fig. 9c only.
1851. *Isotelus* (*Basilicus*) *Powisii* (Murchison) M'Coy *in* Sedgwick & M'Coy, p. 170.
1866. *Asaphus* (*Basilicus*) *powisi* Murchison : Salter, p. 154, pl. 23, figs. 3–7.
1931. *Asaphus powisi* Murchison : Reed, p. 443.
1934. *Parabasilicius powisi* (Murchison) Kobayashi, p. 476.
1935. *Asaphus* (*Parabasilicus*) *powisi* Murchison : Reed, p. 13.
1937. *Parabasilicus powisi* (Murchison) : Kobayashi, p. 503.
1938. *Asaphus* (*Parabasilicus*) *powisi* Murchison : Stubblefield *in* Pocock *et al.*, pp. 89, 255.
1958. *Parabasilicus powisi* (Murchison) : Dean p. 220.
1961. *Parabasilicus powisi* (Murchison) : Dean & Dineley, p. 374, pl. 20, fig. 8.

DESCRIPTION. The species was described first by Murchison (1839 : 661) on the basis of two syntypes. One of these (Murchison, 1839, pl. 23, figs. 9*a*, *b*) has been shown to be a cephalon of *Chasmops extensa* (Boeck) and the other syntype (Murchison, 1839, pl. 23, fig. 9*c*) has been chosen as lectotype (Dean & Dineley, 1961 : 374). The latter specimen is a flattened, large pygidium with six attached thoracic segments, preserved as an external mould and refigured here as a vinyl plastic cast (Pl. 41, fig. 2). The pygidium is large, with frontal breadth 85 mm. and median length 52 mm., though it has been both vertically compressed and slightly sheared sinistrally. The anterior margin is gently convex forwards, whilst the remainder of the outline is broadly subparabolic. The axis is triangular in plan, though this has undoubtedly been exaggerated by crushing, bounded laterally by poorly-defined, straight, axial furrows which are hardly more than broad, shallow depressions. Frontally the axis occupies roughly one-third of the total glabellar breadth, and its anterior third carries traces of three large axial rings : beyond these the axis is virtually smooth, and ends in a slightly better-defined terminal piece, separated from the margin by a long (*sag.*) posterior border. The pleural lobes also have a broad, gently concave, smooth border, inside which the pleural fields are slightly convex dorsally with seven pairs of shallow, poorly-defined pleural furrows becoming progressively fainter posteriorly, the furrowed area extending only for about two-thirds of the length of the axis. Each pleural lobe has a large, steeply downturned, anterolateral facet ; on the lectotype, only the left facet is preserved, slightly distorted by crushing.

The thorax of the lectotype retains only six thoracic segments. Each axial ring is relatively long (*sag.*), transversely straight as far as the poorly-defined axial furrows. What appears, superficially, to be another pair of longitudinal furrows is found on the lectotype (Pl. 41, fig. 2), extending along the thorax and intersecting each axial ring at the points where it is curved backwards. This inner pair of " furrows " is not present on uncrushed specimens assigned to the species, although it is known from individuals which have undergone distortion, and is believed to be of tectonic origin. The thoracic pleurae are directed only slightly backwards distally, and end in blunt tips ; the latter are not preserved on the lectotype, but on other specimens each can be seen to form a small, spine-like posterolateral process which, presumably, functioned as a stop during enrollment. There is a well-defined pleural furrow on each pleura, running from the anterior margin at the axial furrow towards, but not reaching, the posterolateral part of the pleural tip. Immediately in front of this furrow is a parallel ridge which reaches the tip, though in a diminished form, and beyond the ridge the anterior band of the pleura is turned down anterolaterally, again a feature which was probably functional in enrollment.

No topotype cephalon is yet available, and the following description is founded on a cranidium from Pontesford, east Shropshire, which retains the full asaphid complement of eight thoracic segments, and has one associated librigena (Pl. 41, fig. 1). This individual shows the cranidium to be of depressed form, only gently convex both longitudinally and transversely, with straight posterior margin. The glabella is longer than broad in the ratio 4 : 3 and, although the frontal glabellar lobe is moderately well defined anteriorly but with no incised preglabellar furrow, the remainder of the glabella is poorly defined, particularly posteriorly, where it is continuous with the fixigenae and occipital ring. There are no glabellar furrows and the axial furrows are practically obsolete, apart from poorly defined depressions delimiting the lateral margins of the frontal glabellar lobe. The anterior border forms a brim-like structure, its anterior margin moderately convex forwards and its dorsal surface smooth, flattened or slightly concave. The palpebral lobes are strongly curved, placed opposite the middle of the glabella, their dorsal surface flat and continuous with that of the glabella. The anterior branches of the facial suture diverge forwards from the eyes for about half their length, but then curve strongly and evenly inwards to cut the anterior border at an acute angle, longitudinally in-line with the palpebral lobes. The posterior branches are moderately curved backwards from the eyes, and cut the posterior margin of the cephalon midway between the axial furrows and the lateral margins. One displaced librigena has been found in association with the cranidium (Pl. 41, fig. 1), though the visual surface of the eye is too badly damaged for examination. There is a broad, flat platform circumscribing the eye, and from this the remaining dorsal surface of the librigena declines gently to the margin, which is slightly concave, though there is no marginal furrow. The librigena is produced posterolaterally to form a stout, sharp, librigenal spine which extended originally as far as the mid-point of the thorax. None of the available specimens shows any ornamentation of the surface of the test, with the exception of the distal portions of the thoracic pleurae which carry terrace-lines between the pleural tips and the fulcrum. There is no trace of a median tubercle on the glabella, though the exoskeleton has always been found damaged at the point where such a tubercle might be expected to occur.

No hypostoma has yet been recorded from the type-locality, nor has one been found in association with undoubted specimens of *Parabasilicus powisi*. However, a specimen, assigned doubtfully to the species, is figured here from the middle Costonian of the Coston district (Pl. 40, fig. 2). It is preserved as an internal mould, lacks the anterior wings, and is longer than broad in the ratio 6 : 5. The median body is gently convex both longitudinally and transversely, sub-ovate in plan, longer than broad, with a pair of well-defined maculae sited posteriorly, a short distance either side of the axial line. The posterior border is indented by a deep, parabolic notch which extends forwards as far as the median body and is flanked posterolaterally by a pair of broad points. From these points the flattened lateral border runs forwards in a curve, at first expanding and then contracting to meet the sides of the median body just in front of centre.

LECTOTYPE. GSM. 6841 (Pl. 41, fig. 2).

HORIZONS AND LOCALITIES. The lectotype of *Parabasilicus powisi* was obtained from Trilobite Dingle (= Bron-y-Buckley Wood), Welshpool, and is therefore almost certainly of Harnagian age ; this tends to be confirmed by the state of preservation, which resembles that of the so-called Trilobite Dingle Shales. In south Shropshire, the earliest example of the species is from the Costonian Stage of the Evenwood district (Pl. 40, fig. 1) ; this is a smaller specimen than the lectotype, but shows all the specific characters, as far as can be judged, and closely resembles a specimen figured by Salter (1866, pl. 23, fig. 5) from an unspecified horizon at Waterloo Bridge, Conway. Asaphid remains are uncommon in the Harnagian strata of south Shropshire, but a fragmentary cranidium (Pl. 42, fig. 9) and pygidium, B.M. In. 55371, from the *Reuscholithus reuschi* Zone of Smeathen Wood, Horderley, can probably be assigned to *P. powisi*, as also can a relatively small cranidium and pygidium from the same horizon at Coundmoor Brook, Harnage (Pl. 40, figs. 4, 5).

The species *Asaphus* (*Basilicus*) *marstoni* was founded by Salter (1866 : 156, pl. 23, figs. 1*a*, *b*) on a small damaged dorsal shield preserved as an internal mould, together with the damaged right librigena of a slightly larger specimen, both from the " Shales of Horderly ". The syntypes are refigured here (Pl. 42, figs. 1, 6, 8). Although Reed (1931 : 470) claimed that the species was better referred to the genus *Proetus*, there can be little doubt that it is, as Salter believed, an asaphid. Reed's assertion that the specimen represents an immature individual with less than the usual proetid quota of thoracic segments seems to be incorrect, as the eight segments present are typically asaphid in both form and number. The cephalon is damaged but shows nevertheless a general resemblance to that of *Parabasilicus powisi*, as do the pleural lobes of the thorax, though the thoracic axis is more convergent posteriorly than that of the latter species. The pygidium resembles that of *P. powisi* in outline but the axis is better defined and the pleural fields of the pleural lobes are more strongly convex, with at least six pairs of moderately defined pleural furrows, though the number of both these, and the axial rings, present is obscured by abrasion and crushing. In the absence of additional material it seems advisable, for the present, to restrict the name *Parabasilicus* ? *marstoni* to the type-specimens. The preservation of the type-material matches that of the Smeathen Wood Beds, belonging to the Harnagian Stage, of the Onny Valley near Horderley. The only other asaphids known from these strata are probably referable to *Parabasilicus powisi*, and *P.*? *marstoni* may well prove to be a synonym of the former species. The apparent differences could well be explained by variations in preservation or in the stage of development, and the more distinct furrowing of the pygidium of *P.*? *marstoni* may have disappeared by the time the adult stage was attained.

Evidence of *P. powisi* from the Lower Soudleyan, *Broeggerolithus broeggeri* Zone, is scanty, but includes a large pygidium and thorax from Glenburrell Farm (Pl. 40, fig. 3) as well as the cephalon and thorax already described from Habberley Brook, Pontesford. In the succeeding Upper Soudleyan and Lower Longvillian strata, asaphid fragments, especially pygidia, are not uncommon. The pygidium and hypostoma from " Horderley ", figured by Salter (1866, pl. 23, figs. 4, 6) as *Asaphus* (*Basilicus*) *Powisi*, are probably from the Horderley Sandstone. The hypostoma, now refigured (Pl. 42, fig. 2), is proportionately narrower than the Costonian specimen questionably referred here to *P. powisi* (Pl. 40, fig. 2), though bearing a general resemblance to the latter. None of the pygidia from these younger horizons may be satisfactorily matched with that of *P. Powisi*, and they (Pl. 40, fig. 6 ; Pl. 42, fig. 5), together with the hypostoma mentioned, are merely referred, with some uncertainty, to *Parabasilicus*. In general, the Longvillian pygidia, as well as being of slightly different outline, tend to exhibit more ring and pleural furrows than *P. powisi* ; in this respect they resemble the pygidium of *Parabasilicus* ? *marstoni*, already discussed, but until more satisfactory material becomes available specific identification is virtually impossible. The only evidence of asaphid trilobites from the Upper Longvillian of Shropshire is an unidentifiable fragment from the Alternata Limestone, and the family is unknown from all the succeeding strata.

The distribution of *Parabasilicus powisi* and allied forms in the south of Shropshire is of particular interest in that the genus is found most commonly elsewhere in the Chikunsan Beds of South Korea, from which area the type species was described by Kobayashi (1934 : 475). However, another asaphid genus, *Basilicus*, though best known from the Llandeilo Series of Wales, occurs also in Korea (Kobayashi, 1934 : 465). Elsewhere, trilobites assigned to *Parabasilicus* are recorded from both Bolivia and Virginia (Kobayashi, 1937 : 503 ; Raymond, 1925 : 85–86), though the former record has been questioned by Harrington and Leanza (1957 : 36), who tentatively report the genus from Argentina. Most of the Shropshire occurrences of *P. powisi* are in strata correlated with the *Diplograptus multidens* Zone, though known from the top of the preceding *Nemagraptus gracilis* Zone, and extending upwards at least a little way into the succeeding *Dicranograptus clingani* Zone. According to Kobayashi (1934 : 336) the Chikunsan Beds are of Llandeilo age, but as they contain *Diplograptus* (*Amplexograptus*) *perexcavatus* Lapworth, a species said to be common in the Llandeilo and early Caradoc Series of Great Britain (Elles & Wood, 1914 : 521), both they and the Korean species of *Parabasilicus* may be of an age comparable to those of Shropshire. The form most resembling *P. powisi*, as noted by Kobayashi (1934 : 480) is that described by him as *Parabasilicus shirakii* ; the differences between the two are small, the thoracic axis of *P. shirakii* being the narrower, whilst the palpebral lobes are sited farther forwards than in *P. powisi*. Although several specific names were erected by Kobayashi for the material of *Parabasilicus* from Korea, it seems likely that only one or two species are, in fact, present, most of the apparent differences being the result of tectonic distortion or intraspecific variation.

The asaphid trilobite from the Richmond Formation of Ohio described by Foerste (1919 : 65, pls. 14, 14A, 15, especially 15) as *Isotelus brachycephalus* is a large form resembling *Parabasilicus* in some respects, including the anterior facial suture, the shape of the librigenae, the thorax, and the pygidial outline. However, the eyes are situated farther forwards, and the axial and pleural furrows of the pygidium are even less well defined than in the British species.

Family ILLAENIDAE Hawle & Corda, 1847

Genus ***ILLAENUS*** Dalman, 1827

TYPE SPECIES. *Entomostracites crassicauda* Wahlenberg, 1821 by subsequent designation of Miller (1889 : 550).

Illaenus cf. ***fallax*** Holm

(Pl. 42, figs. 3, 4, 12)

1958. *Illaenus* sp., Dean, pp. 211–213, 224.

Several fragments of illaenid trilobites have been recovered from strata of Actonian and Onnian age in south Shropshire. They are often damaged and distorted, but a few of the best preserved are now figured. No undamaged cranidium has been found, and it has not proved possible to make a firm identification of most of those found (Pl. 42, figs. 7, 10, 11). Two pygidia, however, are undistorted and show certain distinctive features (Pl. 42, figs. 3, 4). The outline is well rounded, subparabolic, the median length about three-quarters of the maximum breadth, attained just behind the anterior margin. The axis, occupying about one-quarter of the frontal breadth, is triangular in outline, scarcely defined by faint axial furrows which converge backwards at 50 degrees to meet just in front of centre of the pygidium, and continue back as a single faint furrow for about half the distance to the posterior margin, finally being replaced by an extremely low, thin, median ridge which runs almost to the margin. The dorsal surface of the axis, which bears traces of four or five axial rings, is slightly depressed or level, whilst the surface of the pygidium outside the axial furrows is at first level and then declines fairly steeply towards the margins. The front of the axis is marked by a moderately deep, transversely straight, articulating furrow which turns backwards slightly as it crosses the axial furrows, and then becomes both deeper and markedly broader (*exsag.*), finally terminating at about the proximal margin of the doublure. Immediately in front of this furrow each pleural lobe carries a pronounced, broad (*exsag.*) ridge, bordered frontally by a large, steeply downturned, anterolateral facet.

Illaenus fallax was described by Holm (1882 : 82, pl. 2, figs. 11–20, pl. 5, figs. 15–24) using a number of syntypes stated to be from the " Chasmopskalk " of Sweden ;

several localities are mentioned in his account, and two or more horizons are almost certainly involved. One Shropshire cranidium (Pl. 42, fig. 12) is generally similar to that of *I. fallax*, whilst pygidia figured here bear a remarkably close resemblance to one figured by Holm (1882, Pl. 2, fig. 17) from Gulleråsen, a specimen which possesses also the characteristic axial outline, followed by a median groove and ridge. Thorslund (1940 : 140–141) recorded *Illaenus fallax* from different localities and horizons in Sweden, but he stated that the species occurs most abundantly in the Kullsberg Limestone of Dalecarlia, an horizon generally contemporaneous with those containing the Shropshire specimens.

Although *Illaenus fallax* has been supposed by Jaanusson (1954 : 574) to belong to what he calls the " *Parillaenus*-Gruppe " of *Illaenus s.s.*, some of the specimens which have been assigned to the species bear a certain resemblance to the genus *Stenopareia* Holm, 1886, and *Stenopareia camladica* has recently been described from the Soudleyan Stage of the Shelve Inlier by Whittard (1961 : 216, pl. 30, figs. 10–13).

HORIZONS AND LOCALITIES. Specimens of Actonian age have been found beside the River Onny, in the vicinity of the junction of the river with Batch Gutter ; at various exposures in and around the village of Acton Scott ; and at Gretton Quarry (now filled in), near Cardington. Localities in Onnian strata include the north bank of the River Onny about 63 yards east of its junction with Batch Gutter (*Onnia* ? *cobboldi* Zone) ; and the river bank 100 yards east of the same junction (*Onnia gracilis* Zone).

Family LICHIDAE Hawle & Corda, 1847

Subfamily LICHINAE Hawle & Corda, 1847

Genus ***METOPOLICHAS*** Gürich, 1901

TYPE SPECIES. *Metopias huebneri* Eichwald, 1842 by subsequent designation of Reed (1902 : 62).

Metopolichas? sp.

(Pl. 43, figs. 3, 4, 6, 7)

1938. *Lichas* aff. *verrucosa* (Eichwald), Stubblefield *in* Pocock *et al.*, p. 255.
1958. *Metopolichas* ? aff. *verrucosa* (Eichwald) Dean, p. 218.

Two fragmentary cranidia from the Costonian Stage may tentatively be referred to *Metopoliches*. They are too incomplete to provide a detailed description of the species, but bear a general resemblance to *Metopolichas patriarchus* (Wyatt-Edgell), recently redescribed by Whittard (1961 : 194, pl. 25, figs. 14–17) from west Shropshire. As far as the state of preservation permits, the fragments differ from *M. patriarchus* in having a greater convexity, smaller basal lateral lobes, and straighter longitudinal furrows. Such differences may, however, be nothing more than the consequence of a different mode of preservation, and a full description of the south Shropshire form must await additional material. *M. patriarchus*, although originally described from the Llanvirn Series of Wales, has been found by Whittard in the

Llandeilo Series of the Shelve Inlier, an horizon not appreciably earlier than the Costonian Stage.

Horizon and localities. Zone of *Harknessella subquadrata*, Stevenshill Quarry, by the south-eastern side of the brook, 1,500 yards south-west of Harnage Farm, Harnage. Zone of *Costonia ultima*, the old quarry, now filled in, 650 yards west of Woolston House, Woolston. Both horizons constitute the highest subdivision of the Costonian Stage in, respectively, the northern and southern parts of the Caradoc district.

Subfamily Homolichinae Phleger, 1936

Genus ***PLATYLICHAS*** Gürich, 1901

Type species. *Lichas margaritifer* Nieszkowski, 1857 by original designation of Gürich (1901 : 522).

Platylichas laxatus (M'Coy)

(Pl. 43, figs. 1, 2, 5, 8–12)

1846. *Lichas laxatus* M'Coy, p. 51, pl. 4, fig. 9.
?1846. *Calymene* (?) *forcipata* M'Coy, p. 48, pl. 4, fig. 14 (Pygidium only).
1848. *Lichas laxatus* M'Coy : Salter *in* Phillips & Salter, p. 340, pl. 8, fig. 6.
1851. *Trochurus nodulosus* M'Coy *in* Sedgwick & M'Coy, p. 151, pl. 1, F, fig. 16.
1852. *Lichas nodulosus* (M'Coy) Salter, p. iv.
1854. *Lichas sexspinus* Angelin, p. 74, pl. 38, figs. 7–8*a*.
1854. *Lichas aculeatus* Angelin, p. 75, pl. 38, figs. 11, 11*a*.
1854. *Lichas laxatus* M'Coy : Murchison, p. 201, fig. 29, 5.
1859. *Lichas laxatus* M'Coy : Murchison, p. 223, fig. 44, 5.
1866. *Lichas laxatus* M'Coy : Salter, p. 324, pl. 19, figs. 1–3.
1866. *Lichas segmentatus* Linnarsson, p. 18, pl. 2, fig. 4.
1867. *Lichas laxatus* M'Coy : Murchison, p. 204, fig. 46, 5.
1872. *Lichas laxatus* M'Coy : Murchison, p. 204, fig. 46, 5.
1884. *Lichas laxatus* M'Coy : La Touche, pl. 3, fig. 63.
1885. *Lichas laxata* M'Coy : Schmidt, p. 125, pl. 6, fig. 24.
1906. *Lichas laxatus* M'Coy : Olin, p. 53, pl. 1, figs. 27, 28.
1908. *Lichas laxatus* M'Coy : Wiman, p. 133, pl. 8, fig. 23.
1937. *Platylichas laxatus* (M'Coy) : Phleger, p. 1090.
1938. *Platylichas laxatus* (M'Coy) *pars* : Stubblefield, p. 34.
1939. *Platylichas laxatus* (M'Coy) : Warburg, p. 118, pl. 12, figs. 1–4, 6, 7, 9–12.
1945. *Platylichas laxatus* (M'Coy) : Størmer, p. 417, pl. 4, fig. 15.
1945. *Platylichas laxatus* (M'Coy) : Bancroft, p. 183.
1958. *Platylichas laxatus* (M'Coy) : Dean, p. 224.
1958. *Platylichas laxatus* (M'Coy) : Tripp, p. 579, pl. 85, figs. 3–5.

This oft-quoted Ordovician trilobite species was founded on a single, incomplete, slightly compressed cranidium, preserved in a dark-grey, shaly mudstone. The specimen is in the M'Coy Collection at the National Museum of Ireland, and is refigured here for the first time since M'Coy's original publication (Pl. 43, fig. 10). The outline of the central glabellar lobe is clavate, narrowing posteriorly to a minimum breadth opposite the posterior portions of the bicomposite lateral lobes, which themselves converge backwards at roughly 70 degrees. The central glabellar lobe expands both frontally, constituting the maximum length of the glabella, and transversely, so that it is level with the distal margins of the bicomposite lateral lobes. The short (*sag.*), flattened, anterior border forms a rim which is separated from the central lobe by a shallow, narrow (*sag.*) furrow containing a pair of hypostomal pits opposite the intersection of the axial and longitudinal furrows. The right palpebral lobe is almost completely preserved ; its length is half that of the bicomposite lateral lobe, and carries a conspicuous palpebral furrow. The longitudinal furrows are moderately deep, curved, converging backwards for most of their length, and then diverge to circumscribe the bicomposite lateral lobes. At this point the holotype is broken, but Tripp (1958, pl. 85, fig. 4) has figured a more complete topotype cranidium showing most of the essential features.

Platylichas laxatus was described in considerable detail by Warburg (1939 : 118) on the basis of Norwegian and Swedish material, which she considered to be specifically identical with that from Ireland. There can be no doubt that, at least as far as the cranidium of *P. laxatus* is concerned, there are no significant differences between Irish, Welsh, English and Scandinavian specimens. The pygidium and hypostoma of the south Shropshire and Scandinavian forms are, for all practical purposes, identical but the hypostoma, thorax and pygidium of *P. laxatus* have not yet been described from topotype material. Until this has been done, it seems preferable to follow Warburg's interpretation of the species, though it may eventually prove necessary to recognize several different species or subspecies.

Under the name *Calymene forcipata*, M'Coy (1846, pl. 40, fig. 14) figured from the " Silurian " of " Slieveroe, Rathdrum ", Ireland, a cranidium and pygidium, of which the latter has been generally supposed to represent *Platylichas laxatus*. In order to stabilize the nomenclature of *Calymene forcipata*, the cranidium figured by M'Coy, now housed in the National Museum of Ireland, is here chosen as lectotype, and may be referred to the genus *Flexicalymene*. The pygidium figured by M'Coy is refigured in the present paper (Pl. 43, fig. 9). The specimen is unusually long, but this is due in part to mechanical deformation. Excluding the pleural spines, of which only the third pair is preserved intact, the outline is roughly semi-elliptical. The axis occupies about one-third of the total breadth, and half the length of the pygidium ; it is mainly parallel-sided, but posteriorly becomes tapered and increasingly convex, whilst the terminal piece is poorly defined. Frontally the axial furrows are well defined and almost parallel, but become convergent near the terminal piece of the axis ; beyond the latter they diverge slightly and terminate at the inner margin of the doublure, about halfway to the posterior margin. The axis has two well-defined axial rings with traces of an additional two. The pleural lobes carry three pairs of pleurae, each of which has a pair of well-defined pleural furrows and terminates laterally in a pair of backwardly-directed pleural spines, though the last-named are only partly preserved. It seems advisable to refer this specimen merely to *Platylichas* sp. until further material is available from the original locality.

HOLOTYPE. M'Coy Collection, National Museum of Ireland (Pl. 43, fig. 10).

HORIZON AND LOCALITIES. *Platichas laxatus* has been found at several localities in south Shropshire, almost all of them comprising strata of the Actonian Stage. They include the bed and banks of the River Onny immediately east and west of its junction with Batch Gutter; the section in the upper part of Batch Gutter itself; several points in and around the village of Acton Scott; exposures near Plaish, north-east of Church Stretton; and Gretton Quarry (now filled in), north-east of Cardington. The species has not been found higher than the *Onnia* ? *cobboldi* Zone of the Onnian Stage in Shropshire, at which horizon it occurs at the exposure in the north bank of the Onny, 63 yards east-south-east of its junction with Batch Gutter. Outside Shropshire, *P.* cf. *laxatus* has been recorded from the Pusgillian Stage and highest Onnian of the Cross Fell Inlier.

Family ODONTOPLEURIDAE Burmeister, 1843

Subfamily ODONTOPLEURINAE Burmeister, 1843

Genus ***PRIMASPIS*** R. & E. Richter, 1917

TYPE SPECIES. *Acidaspis primordialis* Barrande, 1852 by original designation of R. & E. Richter (1917 : 466).

Primaspis harnagensis (Bancroft)

(Pl. 44, figs. 1, 4, 6, 8)

1949. *Acidaspis harnagensis* Bancroft, p. 301, pl. 10, figs. 21, 22.
1958. *Primaspis harnagensis* (Bancroft) Dean, p. 201.
1962. *Primaspis harnagensis* (Bancroft) : Dean, p. 122.

DESCRIPTION. The exoskeleton is known only from a few disarticulated cranidia, together with a single, detached librigena and pygidium. The glabella is subparabolic in plan, strongly convex, its upper surface declined frontally, with median length slightly greater than the maximum breadth, measured across the basal glabellar lobes. The frontal glabellar lobe is small, less than one-fifth of the length of the glabella, and bluntly pointed. There are three pairs of glabellar lobes, those of the third pair being the largest, almost oval in plan, slightly divergent forwards, and just over one-third the length of the glabella. The second glabellar lobes are subcircular in plan, about half the size of the third lobes. Both pairs of lobes are defined by deep second and third glabellar furrows which run backwards, and apparently continue, though shallower, so as to circumscribe the second and third lobes. This last feature is known only from internal moulds preserved in mudstones or shales, and may have been exaggerated by crushing. First glabellar lobes are represented by small, tubercle-like projections, delimited frontally by shallow, straight, first glabellar furrows directed only slightly backwards. The axial furrows are curved, strongly convex abaxially, shallowest just behind the line of the second glabellar furrows and then deepening both anteriorly and posteriorly. The anterior border, though incompletely known, is apparently of typical odontopleurid type, narrowest (*sag.*) medially but broadening abaxially, and delimited posteriorly by a poorly-defined furrow. The occipital ring is strongly convex transversely, with straight upper surface; it is longest (*sag.*) medially, almost one-quarter the length of the glabella, but shortens markedly abaxially, at the same time turning sharply forwards anterolaterally to form a pair of distinct occipital lobes. The glabella and occipital ring are separated by a straight, broad (*sag.*), occipital furrow which deepens distally. The fixigenae are strongly convex, standing highest posteriorly, where they are slightly narrower than the basal glabellar lobes, and decline steeply forwards to end opposite the first glabellar lobes. The palpebral lobes, though poorly known, are apparently strongly convex abaxially, with well-defined palpebral furrows and palpebral rims which are continued forwards as eye ridges to join the frontal glabellar lobe. The ocular surface of the eyes is not known. The anterior branches of the facial suture are convergent forwards, and apparently cut the cephalic margin opposite the anterior ends of the axial furrows, though this part of the exoskeleton has not been found well preserved. As far as can be judged from the available material, the posterior branches run from the palpebral lobes, a little in front of the pleuroccipital furrow, backwards to cut the posterior border at the base of the librigenal spines. The single available librigena (Pl. 44, fig. 8) is of typical odontopleurid form, steeply declined distally from the eye towards the raised marginal rim, the latter defined proximally by a deep marginal furrow which ends at the pleuroccipital furrow. The marginal rim is continued posterolaterally to form a librigenal spine, the length of which is at least equal to that of the remainder of the librigena. There are at least thirteen, slender, marginal spines, transversely straight or directed slightly backwards, and increasing in length (*tr.*) towards the genal angle.

The hypostoma and thorax are not known.

The pygidium, excluding marginal spines, is transversely semielliptical in plan, between three and four times as broad (*tr.*) as long. The axis, occupying frontally one-quarter of the maximum breadth, narrows backwards slightly at first, but ends in a small, bluntly pointed terminal piece which reaches the margin. There are three axial rings, the first well defined, the second and third less so. The axial furrows are moderately deep except frontally, where the first axial ring is produced posterolaterally as a pair of strong raised ridges which cross the flat pleural regions and continue beyond the posterior margin as the fifth and largest of seven pairs of spines distributed evenly along the margin. The first four pairs of spines increase in size from small to only slightly shorter than the conspicuous, stout, fifth pair. The sixth and seventh pairs are slender and subparallel backwards.

The surface of the cephalon, excluding most of the furrows, is covered with closely-set granules of small, almost uniform, size. Similar granules ornament the entire dorsal surface of the librigena, including the librigenal spine, but the marginal spines are smooth. The axis and pleural lobes of the pygidium are covered with slightly coarser granules, but the furrows and pleural spines are apparently smooth.

LECTOTYPE, here chosen. BM. In. 42086.

PARATYPE. BM. In. 42087 (Pl. 44, fig. 6).

HORIZON AND LOCALITIES. The type-locality is the Smeathen Wood Beds, Harnagian Stage, *Reuscholithus reuschi* Zone, at the cart-way section near the southern end of Smeathen Wood, Horderley. A single cranidium has also been collected from the same horizon in the north bank of Coundmoor Brook, 1,300 yards south-west of Harnage Farm, Harnage.

DISCUSSION. For convenience the discussion of *Primaspis harnagensis* is grouped with that of *P. caractaci*.

Primaspis caractaci (Salter)

(Pl. 44, figs. 3, 7, 9, 11, 13, 14)

1853. *Acidaspis caractaci* Salter, p. 7.
1857. *Acidaspis caractaci* Salter : Salter, p. 211, pl. 6, figs. 15–17.
1949. *Acidaspis caractaci* Salter : Bancroft, p. 303.
1958. *Primaspis caractaci* (Salter) Dean, pp. 211, 223, 224.
1962. *Primaspis caractaci* (Salter) : Dean, p. 122.

Description. The dorsal exoskeleton, excluding pleural and pygidial spines, is roughly oval in plan, longer than broad approximately in the ratio 3 : 2. The cephalon is transversely semielliptical in plan, more than twice as broad as long. The glabella is steeply declined forwards, almost as broad as long, attaining its maximum breadth just in front of the occipital furrow, whence it narrows markedly to the subparabolic frontal glabellar lobe. There are three pairs of glabellar lobes, those of the basal pair being suboval in plan, moderately divergent forwards, and of large size, about one-third of the glabellar length. The second glabellar lobes are just over half the length of the basal lobes and slightly oval in plan, with long axes parallel to those of the succeeding pair. First glabellar lobes, originally stated by Salter (1857 : 211) to be obsolete, are poorly represented by a pair of small tubercles, the sudden diminution in size between the second and first pair of lobes resulting in a break in the glabellar outline. The second and third glabellar furrows are parallel to one another, deep, bifurcating, and circumscribe the second and third glabellar lobes, which are thus separated from the almost parallel-sided central glabellar lobe. The axial furrows are narrow and curved, convex abaxially, deepening both frontally and posteriorly but becoming shallower medially, opposite the third glabellar furrows. The anterior border is narrow (*sag.*), moderately inclined forwards, broadening laterally, and separated from the glabella by a furrow which increases in depth abaxially. The occipital ring is relatively long (*sag.*), becoming shorter laterally where it forms two distinct occipital lobes and extends forwards to join with the fixigenae ; it is delimited frontally by a broad (*sag.*), transversely straight, occipital furrow which deepens laterally. Each librigena is quadrant-shaped, and its upper surface declines steeply from the eye to a moderately-deep marginal furrow which ends posterolaterally at its intersection with the pleuroccipital furrow. The lateral margin is thickened, ridge-like, produced posterolaterally at the genal angle to form a stout, librigenal spine, the length of which is at least equal to that of the cephalon. The lateral margin carries thirteen, or occasionally fourteen, short (*tr.*) border spines, the hindmost of them almost transversely straight, becoming progressively less divergent forwards.

The hypostoma is not known.

The thorax comprises ten segments. The axis is moderately convex transversely and the pleural lobes are flat as far as the bases of the pleural spines. Each pleura is divided into two bands by a pleural furrow which runs gently backwards distally from the anterior margin of the pleura at its junction with the axial furrow. The anterior pleural band is narrow (*exsag.*), moderately convex, the tip produced laterally into a short (*tr.*) pleural spine. The posterior pleural band is broader (*exsag.*), more convex, ridge-like, produced posterolaterally to give a posterior pleural spine of length almost equal to that (*tr.*) of the pleura itself. The posterior pleural spines become progressively more strongly directed backwards from front to rear of the thorax.

The pygidium, excluding marginal spines, is transversely semielliptical in plan, with straight anterior margin. The axis occupies about one-quarter of the maximum breadth of the pygidium, and its anterior portion is strongly convex dorsally ; the remainder of the axis declines posteriorly and fails to reach the margin, apparently ending in-line with the inner limit of the doublure. There is evidence of at least two axial rings. The first of these is produced, in the form of a pair of large raised ridges, posterolaterally to the margin, beyond which it continues as a pair of stout spines, slightly divergent backwards. In front of these large spines are situated two pairs of small, slender, parallel spines, whilst the posterior margin of the pygidium carries a further three pairs of small spines of similar size and form, parallel to one another and directed straight backwards.

One of the syntypes of *P. caractaci* (Pl. 44, fig. 13) shows the exoskeleton in what may have been the position of rest of the animal on the sea-floor. The occipital ring and pleuroccipital segment are in the same vertical plane, and in this posture the glabella is steeply declined forwards. At the same time the cephalic margins rest on the border spines of the librigenae, the progressive increase in length of the spines posterolaterally assisting in maintaining the position of the cephalon. The thorax is flexed downwards slightly at its midpoint, rising again towards the pygidium which is, in turn, turned down. A comparable condition is known from other groups of trilobites, for example, the Trinucleidae and Calymenidae, and may be posthumous.

The dorsal surface of the glabella, proximal parts of the librigenae, thorax and pygidium, excluding furrows, is mostly covered with coarse granules, the intervening space between the latter being ornamented with granules of smaller size. The glabellar furrows are smooth, but there is a tendency for the smaller granules to persist across the occipital furrow (Pl. 44, fig. 7). Both the lateral border furrow and the lateral border of the cephalon are finely granulate, the granulation extending over part of the border spines, as far as can be judged.

HORIZONS AND LOCALITIES. The earliest specimen of *Primaspis caractaci* known from south Shropshire is a single librigena from the *Onniella reuschi* Zone of the Marshbrookian Stage, just south of Marsh Wood Quarry, Marshbrook. The species becomes much more abundant, however, in the succeeding Actonian Stage, particularly in the more arenaceous facies, though it is rare in the grey mudstone succession of the Onny Valley. Localities include the stream section just south of the waterfall at the western end of Chuney Pool, Acton Scott ; the old quarry 210 yards east of Acton Scott Church ; the stream section by the east side of the road-bridge about 350 yards west-south-west of Hatton ; and the old quarry, now filled in, at Quarry Field, Cardington. The last-named locality yielded the type-specimens of *P. caractaci*, together with numerous other specimens of the species.

SYNTYPES. GSM. 5214 (Pl. 44, fig. 9) ; GSM. 35473 (Pl. 44, fig. 13).

DISCUSSION. The cranidium is of generally similar form in both *Primaspis harnagensis* and *P. caractaci*, but the former species may be distinguished by its shorter occipital ring, narrower glabella and, perhaps, longer basal glabellar lobes. The pygidia of these forms may be separated more easily, that of *P. harnagensis* having two posterior and four anterior pairs of small marginal spines in addition to the single large pair, whilst the pygidium of *P. caractaci* has three posterior and only two anterior pairs of small spines.

The only other species of *Primaspis* described from the Caradoc Series of the Anglo-Welsh area, *P. semievoluta* (Reed, 1910 : 214, pl. 17, figs. 1–3 ; Dean, 1962) from the Longvillian Stage of the Cross Fell Inlier, has a pygidium with two posterior and two anterior pairs of small marginal spines separated by a single pair of large spines. The pygidium is also slightly longer proportionately than that of the two Shropshire species.

The cranidium of *Primaspis ascitus* (Whittington, 1956 : 199, pls. 1, 2), from the Middle Ordovician of Virginia, is relatively broader than that of *P. harnagensis* and bears a remarkably close resemblance to that of *P. caractaci* though the anterior border of the last-named is slightly longer (*sag.*). The pygidium of *P. ascitus* is more easily distinguished and carries, in addition to the largest pair of margin spines, a further five pairs of small spines, three pairs situated anteriorly and the remaining two pairs posteriorly. An unusual feature common to the pygidia of *P. ascitus* and *P. caractaci* is the manner in which the basal part of each of the large pair of spines is expanded so as to merge with the proximal half of the first succeeding small, marginal spine (Pl. 44, fig. 9 ; see also Whittington, 1956, pl. 1, figs. 9, 10).

In a recent paper Whittard (1961 : 203, pl. 27, fig. 12 ; pl. 27, fig. 13) has figured what he calls *Primaspis* cf. *harnagensis* (Bancroft) and *P.* cf. *caractaci* (Salter) from the Spy Wood Grit of the Shelve district, an horizon approximately contemporaneous with the early Harnagian Stage of south Shropshire. The specimens are too fragmentary for certain indentification but appear to be distinct from either of the south Shropshire forms and may represent a new species.

Family OLENIDAE Burmeister, 1843

Subfamily TRIARTHRINAE Ulrich, 1930

Genus ***TRIARTHRUS*** Green, 1832

TYPE SPECIES. *Triarthrus becki* Green, by monotypy (Green, 1832 : 86–87).

Triarthrus cf. ***linnarssoni*** Thorslund

(Pl. 44, figs. 2, 5, 10, 12)

1940. *Triarthrus linnarssoni* Thorslund, p. 128, pl. 12, figs. 4–12.
1945. *Triarthrus* sp., Bancroft, p. 183.
1949. *Triarthrus* sp. Bancroft, map on p. 302.
1958. *Triarthrus* sp., Dean, pp. 213, 225.
1960. *Triarthrus* cf. *linnarssoni* Thorslund : Dean, p. 86.

Three cranidia in varying degrees of completeness, and a single, small, incomplete pygidium, have been examined, all from one locality in south Shropshire. They match the material described by Thorslund (1940 : 128) in both the shape and proportions of the cranidium and in the position of the palpebral lobes. Librigenae of the Shropshire form have not yet been discovered.

The pygidium (Pl. 44, fig. 2) has a broad axis occupying almost half the total breadth, though this proportion may have been exaggerated by crushing, and tapering backwards only slightly, its junction with the posterior margin being indistinct. There are two well-defined axial rings, with a third ring less well defined. The pleural lobes carry at least two, and possibly three, pleural furrows which extend from the axial furrows to the margin, the ribs so defined curving backwards strongly in the same direction. The pygidium of *T. linnarssoni* has not yet been described, and comparison is therefore impossible.

HORIZON AND LOCALITY. *Onnia* Beds, Onnian Stage, *Onnia superba* Zone, at the " Cliff Section " in the north bank of the River Onny, 720 yards west-south-west of Wistanstow Church.

DISCUSSION. Thorslund's type-specimens came from Västergötland and Jemtland, Central Sweden, where the species occurs in both the Upper Chasmops beds and shales of the corresponding *Dicranograptus clingani* Zone. As has been pointed out elsewhere (Dean, 1960 : 85–86), the trilobite assemblage of these Swedish strata is closely comparable with that of the highest Ordovician rocks of the south Shropshire succession.

Family OTARIONIDAE R. & E. Richter, 1926

Genus ***OTARION*** Zenker, 1833

TYPE SPECIES. *Otarion diffractum* Zenker, 1833 by subsequent designation of R. & E. Richter (1926 : 95).

Otarion sp.

(Pl. 45, fig. 1)

1958. *Otarion* sp., Dean, p. 223.

Trilobites which can be assigned broadly to this genus are uncommon in south Shropshire. A few specimens have been found in the middle and upper Marshbrookian and in the Actonian, one of the best preserved, an incomplete cranidium about 2·5 mm. long, being figured here. The glabella is subparabolic in outline, occupies just over two-thirds of the median length, and is strongly inflated, particularly frontally. There is one pair of basal glabellar lobes, in length about two-fifths that of the glabella, from which they are separated by a pair of deep, curved, basal glabellar furrows. The preglabellar field is convex, steeply declined frontally, separated by a broad (*sag.*), well-defined, anterior border furrow from the thick, slightly flattened, anterior border. Both preglabellar field and anterior border are of equal breadth (*sag.*). The fixigenae are only partly preserved but apparently stand highest opposite the anterior part of the basal glabellar lobes, and are declined frontally, where they are continuous with the preglabellar field. The occipital ring, delimited anteriorly by a deep, transversely straight, occipital furrow, is strongly convex transversely, becoming thicker medially where it is directed upwards and slightly backwards.

The surface of the glabella, fixigenae and preglabellar field, excluding the furrows, which are smooth, is covered with conspicuous, coarse tubercles, but that of the anterior border is finely granulate.

HORIZONS AND LOCALITIES. Specimens belonging, apparently, to the same species have been found in the Marshbrookian Stage both at and near Marsh Wood Quarry, Marshbrook; in the stream-section 550 yards south-south-west of Common Farm, Wallsbank; and by the track 2,900 feet north-west of the Methodist Chapel, Cardington. The highest record is from the middle Actonian at the old quarry 210 yards east of St. Margaret's Church, Acton Scott.

Family PROETIDAE Burmeister, 1843

Subfamily PROETIDELLINAE Hupé, 1953

Genus ***PROETIDELLA*** Bancroft, 1949

? *Ogmocnemis* Kielan, 1959.

TYPE SPECIES. *Proetidella fearnsidesi* by original designation of Bancroft (1949: 304).

Proetidella fearnsidesi Bancroft

(Pl. 45, figs. 3–8, 12, 14)

1949. *Proetidella fearnsidesi* Bancroft, p. 304, pl. 10, fig. 23.
1953. *Decoroproetus fearnsidesi* (Bancroft) Přibyl, p. 60.
1958. *Decoroproetus fearnsidesi* (Bancroft): Dean, pp. 201, 219.
?1961. *Ogmocnemis calvus* Whittard, p. 186, pl. 24, fig. 15.
1962. *Proetidella fearnsidesi* Bancroft: Dean, p. 126.

DESCRIPTION. The dorsal exoskeleton of the holotype, the most complete specimen known, is oval in plan, longer than broad in the ratio 9 : 7. The roughly semicircular cephalon occupies one-third the median length of the holotype, with the glabella equal to one-third the cephalic breadth. The holotype is a flattened specimen, preserved in shaly mudstone, and its appearance and proportions are consequently distorted, but in the case of a specimen preserved in sandy limestones of late Costonian age (Pl. 45, figs. 6, 7) the cephalon is convex both longitudinally and transversely, with the glabella occupying half the cephalic breadth. The glabella of the holotype, including occipital ring, is as long as broad; however, the specimen is not only compressed but damaged, and its apparently irregular outline, narrowing forwards to a blunt point, is misleading, though it has been illustrated by Struve (*in* Moore, 1959; fig. 301, 1). The uncrushed glabellar outline is subparabolic, well rounded frontally, and occasionally the anterior half is slightly constricted. Flattened topotype cranidia tend to appear broader, though with the same general outline, and there is some variation in the ratio of length to breadth (Pl. 45, figs. 12, 14). Most of the known cranidia have no glabellar furrows, though one or two bear traces of a basal pair; the conspicuous basal furrows shown in Struve's illustration (*in* Moore, 1959, fig. 301, 1) are the result of crushing. The glabella is circumscribed laterally and frontally by a narrow, moderately-deep furrow representing the conjoined axial and preglabellar furrows. The glabella is preceded by a preglabellar field and anterior border of somewhat variable form. The preglabellar field is flat, varying in length from one-sixth to one-eighth that of the glabella. The line of demarcation between preglabellar field and anterior border is generally poorly defined in topotype material, with no distinct anterior border furrow (Pl. 45, figs. 3, 12, 14), but specimens in a more arenaceous matrix (see, for example, Pl. 45, fig. 5) tend to have a better defined, more steeply upturned, anterior border. The occipital furrow is well defined and moderately deep, flexing forwards a little both medially and laterally. The occipital ring follows a similar course, ending laterally in poorly defined occipital lobes ; its median length is about one-fifth that of the glabella, and in certain rare instances (Pl. 45, fig. 14) there is a small median tubercle. The eyes, the visual surface of which is not known, are elongated, semielliptical in plan, and slightly convergent forwards, equal in length to just over half that of the glabella. They are each delimited laterally by a moderately defined eye platform, and extend forwards from points sited just outside the axial furrows and opposite the occipital furrow. The combined palpebral lobes and fixigenae are thus small and narrow, becoming almost obsolete both anteriorly, immediately in front of the eyes, and posteriorly, where they reach a minimum opposite the pleuroccipital furrow and then expand suddenly to form part of the pleuroccipital segment (Pl. 45, fig. 4). The anterior branches of the facial suture extend only a very short distance forwards from the eyes, parallel to the axial furrows, before becoming suddenly and markedly divergent almost as far as the anterolateral margin where they turn adaxially through a right-angle and cut the margin at points longitudinally in line with the hindmost parts of the axial furrows. The posterior branches run backwards from the eyes, just outside and parallel to the axial furrows, as far as the pleuroccipital furrows ; there they change direction suddenly, running straight outwards and back to cut the posterior margin of the cephalon at points about mid-way between the axial furrows and the lateral margins. The librigenae thus formed are of relatively large size, produced posterolaterally to form long, broad-based librigenal spines, the points of which end in-line with the mid-point of the thorax, between the fifth and sixth thoracic segments.

The hypostoma is unknown.

The thorax of the flattened holotype comprises ten segments, and is divided into three longitudinal lobes of approximately equal breadth by narrow, deep, axial furrows which are parallel from the first to fifth axial rings, beyond which they converge backwards until the breadth (*tr.*) of the tenth axial ring is little more than half that of the first. The axial rings are of the same general shape as the occipital ring, though perhaps a little shorter (*sag.*). The pleurae are transversely straight for the most part, but beyond the fulcra become directed backwards and end in short pleural spines. Each pleura is divided into two bands of unequal breadth (*exsag.*), of which the anterior band is the narrower, by a sharply defined pleural furrow ; each pleural furrow runs slightly backwards distally from the axial furrow, but turns backwards sharply at the fulcrum towards the pleural spine, at the same time becoming markedly shallower.

The pygidium is broadly subparabolic in plan with margin entire, the breadth about two-and-a-half times the median length in the case of the holotype. The tapering axis occupies just over three-quarters of the median length, carries six well-defined axial rings, and ends in a terminal piece of moderate length, with a small postaxial ridge extending to the margin. The doublure is of even breadth, extending inwards from the posterior margin as far as the tip of the axis. Each side-lobe carries four deeply impressed pleural furrows which curve backwards evenly to intersect the lateral margins ; there are, in addition, one or two further pairs of only poorly defined pleural furrows. The pleural ribs so formed carry faintly impressed rib furrows which are not parallel to the pleural furrows, but run backwards only slightly for about three-quarters of their length and then turn sharply back to the margin. Each rib is thus divided into two bands, of which the anterior is the narrower (*exsag.*).

Excluding all furrows the entire dorsal surface of the exoskeleton is ornamented with a series of thin, raised, anastomosing ridges so as to form a Bertillon pattern which is particularly conspicuous on the glabella.

HORIZONS AND LOCALITIES. The holotype is from shaly mudstones of the basal Harnagian, *Reuscholithus reuschi* Zone, in the old cartway near the south end of Smeathen Wood, Horderley, and a few other specimens have been recovered from this locality. *Proetidella fearnsidesi* occurs also, and in small numbers, at the same horizon as exposed 550 yards north-west of Woolston House, Woolston. In the northern part of the Ordovician outcrop in south Shropshire the same species may be found occasionally in the topmost subdivision, the *Harknessella subquadrata* Beds, of the Costonian Stage.

HOLOTYPE. BM. In. 42083 (Pl. 45, fig. 3).

DISCUSSION. It has recently been suggested by Dean (1962) that *Ogmocnemis calvus*, described by Whittard (1961 : 186) from the Lower Soudleyan of the Shelve Inlier, may prove to be synonymous with *P. fearnsidesi*. *O. calvus* was founded on a single specimen, so there is no information concerning variation within the species. The preglabellar field and anterior border are apparently fairly well differentiated, but this may not be of specific significance, particularly in view of the variation in Harnagian specimens of *P. fearnsidesi*, and the two species are regarded here as being probably synonymous. Specimens of *Proetidella* are figured in the present paper from the Upper and, probably, Lower Soudleyan of south Shropshire (Pl. 45, figs. 9–11). They show small differences from *P. fearnsidesi* in glabellar outline and degree of differentiation of the anterior border, but owing to lack of material it has been impossible to demonstrate whether or not these are more than an expression of a different environment and lithology. The specimens, which are closely similar to the holotype of *Ogmocnemis calvus*, are therefore only compared with *P. fearnsidesi*.

There are in the old collections of the Geological Survey & Museum certain specimens, numbered 35614–35616 and 35618–35620, which are labelled *Proetus ovatus*, a manuscript name attributed to Salter. The specimens are typical *Proetidella fearnsidesi*, and the state of preservation suggests that they originated from the Smeathen Wood Beds of the Horderley district.

The Norwegian species *Proetus asellus* (Esmark), from metamorphosed shales of probable Llanvirn age, has been redescribed and figured by Størmer (1940 : 122, pl. 1, fig. 1). The glabella is of more uniform breadth than that of *Proetidella fearnsidesi*, and the anterior border is apparently better differentiated from the long (*sag.*) preglabellar field, though the importance of the latter feature may not be great. However, the general resemblance of the two forms is enough to suggest that *Proetidella*-like trilobites existed earlier than the Caradoc Series, though the group is inadequately known.

Proetidella? sp.

(Pl. 45, fig. 13)

1958. *Proetus* (*s.l.*) sp., Dean, p. 223.

A single proetid cranidium has been recovered from the Upper Cheney Longville Flags, west of the village of Hatton. The glabellar outline is relatively broad, especially posteriorly, becoming broadly convergent frontally towards the well-rounded frontal glabellar lobe after constricting noticeably at about its mid-point. There is a suggestion of a pair of basal glabellar furrows, but as the specimen is somewhat damaged this feature may have been exaggerated by crushing. The anterior border is bluntly pointed medially, gently inclined forwards, separated from the broad (*sag.*), preglabellar field by a shallow, anterior border furrow. The glabella is circumscribed by a conspicuous preglabellar furrow, continuous laterally with deep axial furrows which become shallower medially. Part of the right occipital lobe remains, showing it to be generally similar to that of *Proetidella fearnsidesi*, though perhaps a little broader and situated slightly farther from the axial furrow. There is insufficient material for the erection of a new species, though the specimen is probably specifically distinct from *P. fearnsidesi*.

Horizon and locality. Marshbrookian Stage, *Dalmanella unguis* Zone, about 350 yards north-west of the road bridge situated 350 yards south-west of Hatton, near Acton Scott.

Family Remopleurididae Hawle & Corda, 1847

Genus ***REMOPLEURIDES*** Portlock, 1843

Type species. *Remopleurides colbii* Portlock by subsequent designation of Miller (1889 : 565–566).

Remopleurides warburgae sp. nov.

(Pl. 46, figs. 1, 2)

1958. *Remopleurides* sp. nov., Dean, p. 224.

Diagnosis. Glabella slightly broader than long, broadest posteriorly, narrowing frontally. Glabellar tongue strongly convex, steeply downturned, equal to about half breadth of glabella. Palpebral lobes flattened, narrowing frontally. Three pairs of equispaced glabellar furrows show through test as black lines. Test mainly smooth.

Description. The glabella is moderately convex longitudinally and transversely, almost as long as broad, its greatest breadth occurring to the rear of centre of the main body. The anterior portion of the glabella is convex, including the glabellar tongue, which is strongly arched downwards. The glabellar tongue is about twice as broad as long, its breadth half that of the glabella, and the lateral margins converge slightly towards the almost straight anterior margin. Strong palpebral furrows delimit the palpebral lobes, which narrow frontally and continue forwards as narrow rims to the anterolateral angles of the glabellar tongue. Three pairs of equidistant, parallel, glabellar furrows are present, their position indicated by poorly visible black lines showing through the test ; the first pair is shorter (*tr.*) than the second and third pairs, which are of almost equal length. The glabellar furrows curve gently backwards from near the palpebral furrows so as to leave an unfurrowed band extending along the axis of the glabella and occupying about one-fifth of the maximum breadth. The occipital furrow is deeply incised and transversely straight. The occipital ring is moderately convex both longitudinally and transversely, but in the holotype the distal parts are not wholly preserved. The surface of the cranidium is smooth except for the occipital ring, palpebral lobes and anterior portion of the glabellar tongue, all of which are ornamented with fine, slightly-raised, anastomosing ridges, sometimes forming a Bertillon pattern.

The hypostoma, thorax and pygidium are not known (but see later).

HORIZON AND LOCALITIES. The type-material was collected from grey mudstones in the uppermost third of the Actonian Stage in the north bank of the River Onny, 87 feet east of the junction of the river with Batch Gutter. The same species occurs also in the Actonian Stage at Acton Scott, and, perhaps, near Hatton.

HOLOTYPE. BM. In. 49751 (Pl. 46, figs, 1, 2).

DISCUSSION. In plan the glabella of *Remopleurides warburgae* most resembles *R. dalecarlicus* Holm MS., described and figured by Warburg (1925 : 88, pl. 1, figs. 7, 8) from the Upper *Leptaena* Limestone of Sweden and therefore younger than the Shropshire species ; the Swedish form also has a smooth test but possesses a narrower, more convex, glabellar tongue.

Remopleurides latus Olin **onniensis** subsp. nov.

(Pl. 46, figs. 4, 5)

DIAGNOSIS. Glabella broader than long, with main body transversely ovate in plan. Glabellar tongue equal in breadth to half that of glabella, strongly declined frontally, its anterior margin transversely truncated and indented medially. Palpebral lobes narrow forwards, forming rim along sides of anterior glabellar tongue. Three pairs glabellar furrows visible through test as dark lines.

DESCRIPTION. The glabella is moderately convex both longitudinally and transversely, its length (*sag.*) equal to three-quarters the maximum breadth, which occurs midway between the occipital furrow and the base of the glabellar tongue. The latter is longitudinally convex, less so transversely, and strongly arched down frontally, its breadth half that of the glabella. Apart from a small median indentation the anterior margin of the glabellar tongue is transversely straight, meeting the anterolateral margins at right-angles. Three pairs of equidistant glabellar furrows are present, showing through the test as poorly-discernible dark lines, and not impressed upon the outer surface of the test. The first pair is shorter (*tr.*) than the second and third pairs which extend distally almost to the palpebral furrows ; the third pair curves backwards a little more strongly than the first and second pairs, which are almost parallel to one another. All three pairs of furrows curve gently backwards and extend adaxially from the lateral margins so as to leave an unmarked band, running down the centre of the glabella and about one-fifth the breadth of the latter. The palpebral lobes, which narrow frontally and are separated from the main body of the glabella by deeply-incised palpebral furrows, continue forwards in the form of a much attenuated rim as far as the anterolateral angles of the glabellar tongue. The occipital ring is only slightly convex longitudinally, and becomes shorter (*exsag.*) laterally. The surface of the test of the glabellar tongue and occipital ring is ornamented with fine, anastomosing, raised ridges arranged parallel to the anterior margin, but the remainder of the test is smooth. The hypostoma, thorax and pygidium are not known (but see later).

HORIZON AND LOCALITIES. The uppermost third of the Actonian Stage, exposed in the north bank of the River Onny, 87 feet east of the junction of the river with Batch Gutter. The type-material was found in a band of shelly débris, about 3 inches thick, containing also *Remopleurides warburgae, Tretaspis, Chasmops, Sampo* and *Onniella*. The species is not known with certainty elsewhere, but fragments possibly belonging to it have been found in the Actonian Stage at Acton Scott.

HOLOTYPE. BM. In. 49750 (Pl. 46, figs. 4, 5).

PARATYPE. BM. In. 49762.

DISCUSSION. The new subspecies is generally similar to *Remopleurides latus* (Olin, 1906, pl. 2, figs. 5*a*, *b*) from the Chasmops Series of Scania, particularly in the form of the posterior half of the glabella, but the convexity of the glabella is greater and the glabellar tongue is both longer and broader. *R. latus kullsbergensis* (Warburg, 1925 : 83, pl. 1, figs. 1–6) has more distinct glabellar furrows as well as a smaller, narrower glabellar tongue than the Shropshire subspecies, though the two are probably of generally similar age, whilst *R. latus* var. *granensis* (Størmer, 1945 : 408, pl. 4, fig. 4), from a slightly higher horizon, differs in possessing a narrower glabellar tongue, and a test which is described as having a completely smooth surface. *R. validus* (Thorslund, 1940, pl. 7, figs. 1–9), from the Lower Chasmops Limestone, shows a glabella of generally similar outline to that of the new subspecies but the glabellar tongue is both narrower and less well differentiated from the main body of the glabella. *R. wimani* (Thorslund, 1940 : 135, pl. 7, fig. 10), though of an age generally comparable to that of *R. latus onniensis*, exhibits a much narrower glabellar tongue and the main body of the glabella is both narrower and more convergent forwards.

Remopleurides sp.

(Pl. 46, figs. 3, 7)

At the type-locality of *Remopleurides warburgae* and *R. latus onniensis*, isolated fragments of *Remopleurides* have been found in abundance in a fossiliferous band of shelly mudstone about 3 inches thick. There appears to have been some sorting of the trilobite remains and although librigenae and thoracic segments are not uncommon, no pygidium has yet been found. Two typical specimens are figured here, but it has not yet been possible to assign either to a definite species.

The main part of the librigena is subtriangular in outline (Pl. 46, fig. 3), slightly convex, and arched down laterally. A long, stout spine is developed, the whole of which is not preserved ; as in the case of *Remopleurides latus kullsbergensis* (Warburg, 1925 : 84, fig. 15), this is not developed from the true genal angle but arises from a position just in front of it. The posterior portion of the librigena stands at a somewhat lower level than the remainder, from which it is separated by a strong transverse furrow. This part of the librigena terminates posterolaterally in a short, blunt, librigenal spine, separated by a well-defined notch from the long anterior spine, but the proximal end is marked by a rounded, flange-like notch, the function of which is to provide articulation with the fulcral process of the first thoracic segment. The surface of the test is ornamented with several well-developed, anastomosing ridges, subparallel to the distal margin of the librigena as far as the genal angle, but transverse in direction near the fulcral notch. The librigena strongly resembles that of *R. latus kullsbergensis* and may belong to the allied *R. latus onniensis*. It also recalls, but is shorter and broader than, one figured by Thorslund (1940, pl. 7, fig. 16) and referred by him to *R.* cf. *latus* Olin.

In addition to numerous isolated thoracic segments, a group of six articulated segments has been found (Pl. 46, fig. 7). The axial rings are gently convex longitudinally and transversely, the breadth at least four times the length (*sag.*), excluding the articulating half-ring. Apart from a small, central portion the posterior margin of each axial ring is serrated, particularly distally, up to six tooth-like spines being visible on the lateral half of each ring ; similar structures are developed on the axial rings of *Remopleurides colbii* Portlock (Whittington, 1950, pl. 70, figs. 1, 4). The side-lobes are narrow, with flattened pleurae terminating in short (*exsag.*), broad, backwardly-directed pleural points. The pleural furrows are curved, deep, directed distally towards, but not attaining, the pleural points. Just outside the axial furrow the anterior margin of each pleura is thickened markedly to form a conspicuous, tooth-like, fulcral process, the posterior margin being indented to give a corresponding, flange-like, articulating socket. The test is ornamented with fine raised ridges distributed more or less parallel to the margins of each segment and tending to converge at the pleural points.

Horizon and locality. Actonian Stage, north bank of the River Onny, 87 feet east of its junction with Batch Gutter.

Genus ***REMOPLEURELLA*** nov.

Diagnosis. Cranidium of typical remopleuridid outline, the main body only gently convex, both longitudinally and transversely, with three pairs of deeply-incised glabellar furrows, those of the first pair noticeably shorter (*tr.*) than those of the other two pairs. Surface of test with conspicuous pattern of subconcentric, thin, raised lines. Librigenae narrow with librigenal spines arising from the genal angles ; posterior margin entire. Hypostoma as long as, or slightly longer than, broad, with transversely straight anterior and posterior borders. Median body suboval, gently convex, with pair of oval areas converging backwards medially ; small anterior lobe, sometimes produced to form short spine, delimited by broad, curved median furrow, convex backwards. Thorax incompletely known. Pygidium unknown.

Robergiella, type-species *R. sagittalis*, from the Edinburg Limestone of Virginia (Whittington, 1959 : 431, pl. 6, figs. 16–33), may be related to *Remopleurella*, which it resembles in the depressed glabellar form, with three incised pairs of glabellar furrows. *Robergiella* differs, however, in having a larger glabellar tongue which expands forwards, as well as considerably broader librigenae, each of which carries a pronounced notch at the base of the librigenal spine.

TYPE SPECIES. *Remopleurides burmeisteri* Bancroft, 1949.

DISTRIBUTION. Known with certainty from the Onnian Stage of the type Caradoc Series in south Shropshire. Probably occurs also in the higher Caradoc strata of southern Norway.

Remopleurella burmeisteri (Bancroft)

(Pl. 45, fig. 2 ; Pl. 46, figs. 6, 8, 9, 11, 12)

1945. *Remopleurides* (? *Caphyra*) sp., Lamont, p. 118.
1949. *Remopleurides burmeisteri* Bancroft, p. 300, pl. 10, figs. 19, 20.
1958. *Remopleurides burneisteri* Bancroft : Dean, pp. 213, 225.

Bancroft's original description covered the cranidium, librigenae and thorax (*pars*), and little need be added. Most known cranidia, including one of the syntypes, are slightly flattened with the glabellar tongue apparently arched down only slightly, but occasional specimens show that the plane of the tongue is, in fact, steeply declined frontally, almost at right-angles to the remainder of the glabella. Most of the known specimens are preserved in decalcified mudstones in which the glabellar test is not seen, but one specimen, BM. In. 54772, from the unweathered underlying strata shows the test to have been thin, its dorsal surface, apart from the smooth, deeply-incised glabellar furrows, ornamented by thin, raised, anastomosing ridges forming a Bertillon pattern.

A hypostoma presumed to belong to this species occurs in association with the paratype thorax, and a slightly smaller specimen has recently been collected by Mr. S. F. Morris. The entire hypostoma is as long as, or slightly longer than, wide. The gently convex median body is generally ovate in outline with bluntly terminated anterior and posterior margins, and is circumscribed by a moderately-deep border furrow. The posterior border is apparently continuous with the narrow (*tr.*) lateral border, which is, in turn, continuous with the anterior border. The last-named is transversely straight produced distally to form a pair of anterior wings, separated by rounded lateral notches from the lateral borders. The median body is divided into two unequal parts by a curved median furrow, concave forwards, deepest medially, and shallowing distally. The anterior lobe is small, convex, and specimen In. 56800 shows it thickened medially to produce a small spine. The posterior lobe, occupying about three-quarters of the length of the median body, is traversed longitudinally by a faint groove, a continuation of the median furrow, which narrows backwards and ends at the posterior border. The posterior lobe is thus divided so as to form what Whittington (1950 : 541) has described as two oval areas, their long axes convergent backwards. Fragments of the test show it to be thin, its lower surface covered by subconcentric, thin, raised ridges.

LECTOTYPE, here chosen. BM. In. 42106 (Pl. 46, fig. 11).

PARATYPES. BM. In. 42098 (Pl. 46, fig. 6); BM. In. 49561 (Pl. 46, figs. 8, 12).

HORIZONS AND LOCALITIES. The earliest known occurrence of the species is a single cranidium, BM. In. 54772, from the Onnian Stage, *Onnia gracilis* Zone, by the north bank of the River Onny about 100 yards east of the junction of the river with Batch Gutter. All the other known specimens, including the types, are from the *Onnia superba* Zone in the north bank of the Onny, 720 yards west-south-west of Wistanstow Church.

DISCUSSION. *Remopleurella burmeisteri* appears to belong to a group of remopleuridid trilobites which, although they have received little attention, are not uncommon in at least the Upper Chasmops Limestone, Stage 4bδ, of southern Norway, and probably occur also in parts of Sweden. Several such are housed in the Paleontologisk Institut, Oslo, where some have been labelled as ' *Remopleurides* cf. *radians* ", the type-species of *Amphitryon* Hawle & Corda, but they cannot be assigned to the latter genus and probably belong to *Remopleurella*.

Family THYSANOPELTIDAE Hawle & Corda, 1847

Genus *EOBRONTEUS* Reed, 1928

TYPE SPECIES. *Entomostracites laticauda* Wahlenberg, 1818 by original designation of Reed (1928 : 58, 75).

Eobronteus? sp.

(Plate 46, fig. 10)

1958. *Eobronteus* ? sp., Dean, p. 224.

Three fragmentary specimens housed in the Sedgwick Museum are the only representatives of this trilobite family found in south Shropshire, and the best preserved of these is now figured. The specimen comprises an almost complete thorax, the full number of thoracic segments not being visible, together with a fragmentary cephalon, which partly obscures the thorax, and an incomplete pygidium. The genus *Eobronteus* has been examined in detail by Sinclair (1949) who has figured or noted all the known species. None of these agrees wholly with the Shropshire species, which may be new, but a detailed description must await the collection of better-preserved material.

HORIZON AND LOCALITY. Onnian Stage, *Onnia superba* Zone, north bank of the River Onny, 720 yards west-south-west of Wistanstow Church.

REFERENCES

ANGELIN, N. F. 1854. *Palaeontologia Scandinavica.* ix + 92 pp., 42 pls. Lund.

BANCROFT, B. B. 1945. The brachiopod zonal indices of the Stages Costonian to Onnian in Britain. *J. Paleont.*, Tulsa, **19** : 181–252, pls. 22–38.

—— 1949. Upper Ordovician trilobites of zonal value in south-east Shropshire. *Proc. Roy. Soc.*, London (B) **136** : 291–315, pls. 9–11. (Edited by A. Lamont).

BARRANDE, J. 1852. *Système silurien du centre de la Bohême. 1 ère partie. Recherches paléontologiques.* xxx + 935 pp., atlas, 51 pls. Prague & Paris.

DEAN, W. T. 1958. The faunal succession in the Caradoc Series of south Shropshire. *Bull. Brit. Mus. (Nat. Hist.) Geol.*, London, **3** : 191–231, pls. 24–26.

—— 1959. The stratigraphy of the Caradoc Series in the Cross Fell Inlier. *Proc. Yorks. Geol. Soc.*, Hull, **32** : 185–228, 6 figs.

—— 1960. The use of shelly faunas in a correlation of the Caradoc Series in England, Wales and parts of Scandinavia. *Proc. Int. Geol. Congr., 21st Session*, Copenhagen, **7** : 82–87.

—— 1960*a*. The Ordovician rocks of the Chatwall district, Shropshire. *Geol. Mag., Lond.*, **97** : 163–171, 2 figs.

—— 1962. The trilobite faunas of the Caradoc Series in the Cross Fell Inlier of Northern England. *Bull. Brit. Mus. (Nat. Hist.), Geol.*, London, **7** : 65–134, pls. 6–18.

DEAN, W. T. & DINELEY, D. L., 1961. The Ordovician and associated Pre-Cambrian rocks of the Pontesford district, Shropshire. *Geol. Mag., Lond.*, **98** : 367–376, pl. 20.

ELLES, G. L. & WOOD, E. M. R. 1914. A Monograph of British Graptolites, **10** : 487–526, pls. 50–52. *Palaeontogr. Soc.* [*Monogr.*], London.

FOERSTE, A F. 1919. Notes on *Isotelus, Acrolichas, Calymene* and *Encrinurus*. *Bull. Sci. Labs. Denison Univ.*, Granville, Ohio, **19** : 65–81, pls. 14–18.

GREEN, J. 1832. *A Monograph of the Trilobites of North America : with coloured models of the species.* 93 pp., 1 pl. Philadelphia.

GÜRICH, G. 1901. Über eine neue *Lichas*-Art aus dem Devon von Neu Süd-Wales und über die Gattung *Lichas* überhaupt. *N. Jb. Min. Geol. Paläont.*, Stuttgart, **14** : 519–539, pls. 18–20.

HARPER, J. C. 1947. The Caradoc fauna of Ynys Galed, Caernarvonshire. *Ann. Mag. Nat. Hist.*, London (11) **14** : 153–175, pls. 6, 7.

HARRINGTON, H. J. & LEANZA, A. F. 1957. Ordovician trilobites of Argentina. *Dept. Geol. Univ. Kansas, Spec. Pub.*, Lawrence, **1** : 1–276, 140 figs.

HAWLE, I. & CORDA, A. J. C. 1847. *Prodrom einer Monographie der böhmischen Trilobiten.* 176 pp., 7 pls. Prague. (Published also 1848, *Abh. K. böhm. Ges. Wiss.*, Prague, **5** : 117–292, pls. 1–7).

HOLM, G. 1882. De Svenska arterna af Trilobitslägtet *Illaenus* (Dalman). *K. svenska Vetensk-Akad. Handl.*, Stockholm, **7** : xiv + 136 pp., 6 pls.

JAANUSSON, V. 1954. Zur Morphologie und Taxonomie der Illaeniden. *Ark. Min. Geol.*, Stockholm, **1** (20) : 545–583, pls. 1–3.

KOBAYASHI, T. 1934. The Cambro-Ordovician formations and faunas of South Chosen, Part I : Middle Ordovician faunas. *J. Fac. Sci. Univ. Tokyo* (2) **3** : 329–519, pls. 1–44.

—— 1937. The Cambro-Ordovician shelly faunas of South America. *J. Fac. Sci. Univ. Tokyo* (2) **4** : 369–522, pls. 1–8.

LAMONT, A. 1945. Excursion to Onny River, Shropshire. *Quarry Manager's J.*, Mexborough, **29** : 118–119, 1 fig.

LA TOUCHE, J. D. 1884. *A Handbook of the Geology of Shropshire.* 99 pp., 22 pls. London & Shrewsbury.

LINNARSSON, J. G. O. 1866. Om de Siluriska Bildningarne i Mellersta Westergötland. I. 23 pp. 2 pls. Stockholm.

M'COY, F. 1846. *A synopsis of the Silurian fossils of Ireland.* 68 pp., 4 pls. Dublin.

MILLER, S. A. 1889. *North American geology and paleontology.* 795 pp., 1457 figs. Cincinnati.

MILLER, A. K., YOUNGQUIST, W. & COLLINSON, C. 1954. Ordovician Cephalopod fauna of Baffin Island. *Mem. Geol. Soc. Amer.*, Baltimore, **62** : 1–234, pls. 1–63.

MOORE, R. C. 1959. *Treatise on Invertebrate Paleontology. Part O. Arthropoda 1.* xix + 560 pp., 415 figs. Lawrence & Meriden.

MURCHISON, R. I. 1839. *The Silurian System, founded on geological researches in the counties of Salop, Hereford, Radnor, Montgomery, Caermarthen, Brecon, Pembroke, Monmouth, Gloucester, Worcester and Stafford ; with descriptions of the coal-fields and overlying formations.* xxxii + 768 pp., 40 pls., London.

MURCHISON, R. I. 1854. *Siluria.* xv + 523 pp., 37 pls. London.

—— 1859. *Siluria.* 3rd edit. xix + 592 pp., 41 pls. London.

—— 1867. *Siluria.* 4th edit. xvii + 566 pp., 41 pls. London.

—— 1872. *Siluria.* 5th edit. xvii + 566 pp., 41 pls. London.

OLIN, E. 1906. Om de chasmopskalken och trinucleusskiffern motsvarande bildningarna i Skåne. *Lund. Univ. Årsskr.* (N.F., 2), **2** : 1–79, pls. 1–4.

PHLEGER, F. B. 1937. Species and geographic distribution of the Lichadacea. *Amer. Midl. Nat.*, Notre Dame, **18** : 1085–1092.

PHILLIPS, J. & SALTER, J. W. 1848. Palaeontological Appendix to Professor John Phillips' Memoir on the Malvern Hills, compared with the Palaeozoic Districts of Abberley, &c. *Mem. Geol. Surv. Gt. Britain,* London, **2**, 1 : 331–386, pls. 4–30.

POCOCK, R. W., WHITEHEAD, T. H., WEDD, C. B. & ROBERTSON, T. 1938. Shrewsbury District, including the Hanwood Coalfield (One-inch Geological Sheet 152 New Series). xii + 297 pp., 8 pls. *Mem. Geol. Surv. Gt. Britain,* London.

PŘIBYL, A. 1953. Seznam českých trilobitových rodů (Index of trilobite genera in Bohemia). *Knihovna Ustř. úst. geol.*, Prague, **25** : 1–80. (In Czech, Russian and English).

RAYMOND, P. E. 1925. Some trilobites of the lower Middle Ordovician of eastern North America. *Bull. Mus. Comp. Zool. Harv.*, Cambridge, Mass., **67** : 1–180, pls. 1–10.

REED, F. R. C. 1902. Notes on the genus *Lichas*. *Quart. J. Geol. Soc. Lond.*, **58** : 59–82, 19 figs.

—— 1906. The Lower Palaeozoic Trilobites of the Girvan District, Ayrshire. **3** : 97–186, pls. 14–20. *Palaeontogr. Soc.* [*Monogr.*], London.

—— 1910. New fossils from the Dufton Shales. *Geol. Mag. Lond.* (5) **7** : 211–220, 294–299, pls. 16, 17, 23, 24.

—— 1928. Notes on the Bronteidae [= Goldiidae]. *Ann. Mag. Nat. Hist.*, London (10) **1** : 49–78.

—— 1931. A review of the British species of the Asaphidae. *Ann. Mag. Nat. Hist.*, London (10) **7** : 441–472.

—— 1935. The Lower Palaeozoic Trilobites of Girvan, Supplement No. 3 : 1–64, pls. 1–4. *Palaeontogr. Soc.*, [*Monogr.*], London.

RICHTER, R. & E. 1917. Über die Einteilung der Familie Acidaspidae und über einige ihrer devonischen Vertreter. *Zbl. Miner.*, Stuttgart, **1917** : 462–472, 10 figs.

—— 1926. Beiträge zur Kenntnis devonischer Trilobiten, IV. Die Trilobiten des Oberdevons. *Abh. preuss. geol. Landesanst.*, Berlin (N.F.) **99** : 1–314, pls. 1–12.

SALTER, J. W. 1852. A systematic description of Palaeozoic fossils in the Geological Museum of the University of Cambridge. Appendix A. Description of a few species from Wales and Westmorland referred to in the foregoing work. Appendix to Sedgwick & M'Coy, 1851 : i–viii.

—— 1853. Figures and descriptions illustrative of British organic remains. *Mem. Geol. Surv. U.K.*, London, Dec. **7** : 1–78, pls. 1–10.

—— 1857. On two Silurian species of *Acidaspis* from Shropshire. *Quart. J. Geol. Soc. Lond.*, **13** : 210–211, pl. 6.

—— 1865. On the fossils of North Wales. Appendix to Ramsay, A. C., The geology of North Wales. *Mem. Geol. Surv. Gt. Britain,* London, **3** : 239–363, pls. 1–26.

—— 1865*a*. A Monograph of the British Trilobites from the Cambrian, Silurian, and Devonian formations, **2** : 81–128, pls. 7–14. *Palaeontogr. Soc.* [*Monogr.*], London.

—— 1866. A Monograph of the British Trilobites from the Cambrian, Silurian and Devonian formations, **3** : 129–176, pls. 15–25. *Palaeontogr. Soc.* [*Monogr.*], London.

SCHMIDT, F. 1885. Revision der ostbaltischen silurischen trilobiten nebst geognostischer übersicht des ostbaltischen Silurgebiets, II. Acidaspiden und Lichiden. *Mém. Acad. Imp. Sci. St. Pétersb.* (7) **33** : 1–127, pls. 1–6.

SEDGWICK, A. & M'COY, F. 1851. *A synopsis of the classification of the British Palaeozoic rocks, with a systematic description of the British Palaeozoic fossils in the geological museum of the University of Cambridge, I.* iv + 184 pp., 11 pls. London & Cambridge.

SHIRLEY, J. 1931. A redescription of the known British Ordovician species of *Calymene* (*s.l.*). *Mem. Proc. Manchr. Lit. Phil. Soc.*, **75** : 1–35, pls. 1, 2.

—— 1936. Some British trilobites of the Family Calymenidae. *Quart. J. Geol. Soc. Lond.*, **92** : 384–422, pls. 29–31.

—— 1938. The fauna of the Baton River Beds (Devonian), New Zealand. *Quart. J. Geol. Soc. Lond.*, **94** : 459–505, pls. 40–44.

SINCLAIR, G. W. 1949. The Ordovician trilobite *Eobronteus*. *J. Paleont.*, Menasha, **23** : 45–56, pls. 12–14.

STØRMER, L. 1940. Early descriptions of Norwegian trilobites. The type specimens of C. Boeck, M. Sars and M. Esmark. *Norsk. geol. Tidsskr.*, Oslo, **20** : 113–151, pls. 1–3.

—— 1945. Remarks on the *Tretaspis* (*Trinucleus*) Shales of Hadeland, with descriptions of trilobite faunas. *Norsk. geol. Tidsskr.*, Oslo, **25** : 379–426, pls. 1–4.

STUBBLEFIELD, C. J. 1938. The types and figured specimens in Phillips and Salter's Palaeontological Appendix to John Phillips' memoir on " The Malvern Hills compared with the Palaeozoic districts of Abberley, etc." (*Mem. Geol. Surv.*, Volume II, Part I, June 1848). *Summ. Progr. Geol. Surv.*, London for 1936, Pt. II : 27–51.

THORSLUND, P. 1940. On the Chasmops Series of Jemtland and Södermanland (Tvären). *Sverig. geol. Unders. Afh.*, Stockholm (C) **436** : 1–191, pls. 1–15.

TRIPP, R. P. 1958. Stratigraphical and geographic distribution of the named species of the trilobite Superfamily Lichacea. *J. Paleont.*, Tulsa, **32** : 574–582. pl. 85.

WARBURG, E. 1925. The trilobites of the Leptaena Limestone in Dalarne, with a discussion of the zoological position and the classification of the Trilobita. *Bull. geol. Instn. Univ. Uppsala,* **17** : i–viii, 1–446, pls. 1–11.

—— 1939. The Swedish Ordovician and Lower Silurian Lichidae. *K. svenska VetenskAkad. Handl.*, Stockholm, **17**, 4 : 1–162, pls. 1–14.

WHITTARD, W. F. 1960. The Ordovician trilobites of the Shelve Inlier, West Shropshire, **4** : 117–162, pls. 16–21. *Palaeontogr. Soc.* [*Monogr.*], London.

—— 1961. The Ordovician trilobites of the Shelve Inlier, West Shropshire, **5** : 163–196, pls. 22–25. *Palaeontogr. Soc.* [*Monogr.*], London.

WHITTINGTON, H. B. 1950. Sixteen Ordovician genotype trilobites. *J. Paleont.*, Tulsa, **24** : 531–565, pls. 68–75.

—— 1956. Silicified Middle Ordovician trilobites : the Odontopleuridae. *Bull. Mus. Comp. Zool. Harv.*, Cambridge, Mass., **114** : 155–288, pls. 1–24.

—— 1959. Silicified Middle Ordovician trilobites : Remopleurididae, Trinucleidae, Raphiophoridae, Endymionidae. *Bull. Mus. Comp. Zool. Harv.*, Cambridge, Mass., **121** : 371–496, pls. 1–36.

WIMAN, G. 1908. Studien über das Nordbaltische Silurgebiete. *Bull. Geol. Instn. Univ. Uppsala.*, **8** : 73–168, pls. 5–8.

PLATES

Specimens whitened with ammonium chloride before photographing. Numbers with prefixes BM. In., GSM., and A. are housed respectively in the British Museum (Natural History), London, the Geological Survey & Museum, London, and the Sedgwick Museum, Cambridge. Other figured specimens are in the Shrewsbury Museum and the National Museum of Ireland, Dublin.

PLATE 37

Flexicalymene acantha Bancroft . . . . p. 216

Harnagian Stage, zone of *Reuscholithus reeuschi*, section in old cartway, near southern end of Smeathen Wood, near Horderley.

FIG. 1. Internal mould of cephalon with incomplete thorax. BM. In. 50635. ×2.

FIG. 3. Lectotype, an immature cranidium preserved as an internal mould. BM. In. 42091. ×3.

FIG. 4. Paratype pygidium, an internal mould. BM. In. 49592. ×3.

FIGS. 5, 6. Latex cast from external mould of adult cranidium. BM. In. 50622. ×2.

FIG. 14. Latex cast from external mould of damaged, almost whole, dorsal exoskeleton. BM. In. 50623. ×2·5.

Flexicalymene cf. *acantha* Bancroft . . . . p. 217

Costonian Stage, zone of *Costonia ultima*, old quarry about 500 feet south of Coston Farm, 1 mile east of Clunbury.

FIG. 7. Internal mould of cranidium showing glabellar outline. BM. In. 51694. ×2.

FIG. 10. Cranidium illustrating variation in glabellar outline. BM. In. 52226. ×2.

FIG. 13. Internal mould of pygidium, with axis broadened by crushing. BM. In. 52227. ×2.

Flexicalymene (*Reacalymene*) *horderleyensis* sp. nov. . . p. 221

Lower Longvillian Substage, zone of *Dalmanella indica* and *D. lepta*, south-eastern corner of Rookery Wood, south-east of Horderley.

FIGS. 2, 8. Latex cast of holotype, an external mould. BM. In. 50656. ×2.

Flexicalymene planimarginata (Reed) . . . . p. 217

Lower Longvillian Substage, zone of *Dalmanella horderleyensis*, Long Lane Quarry, ¾ mile north-west of Craven Arms.

FIG. 15. Internal mould of pygidium. BM. In. 52104. ×2·3.

Flexicalymene (*Reacalymene*) *pusulosa* (Shirley) . . . p. 220

Costonian Stage, probably zone of *Harknessella subquadrata*, quarry near eastern end of Black Dick's Coppice, Evenwood.

FIGS. 9, 11. Holotype cranidium with test preserved. BM. In. 50780. ×2·5.

Horizon as for Fig. 9. Old quarry in north-western part of Round Nursery, south of Harnage Grange.

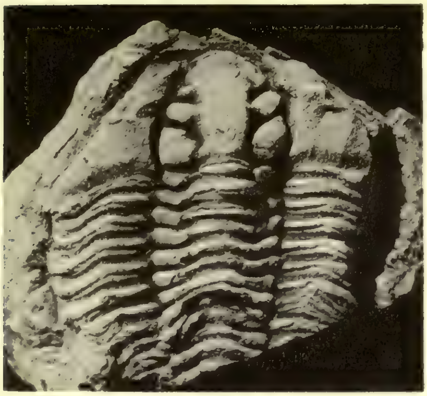
FIG. 12. Pygidium showing granulate surface. BM. In. 54868. ×3.

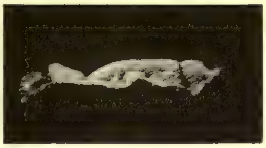
Flexicalymene (*Reacalymene*) cf. *limba* (Shirley) . . p. 221

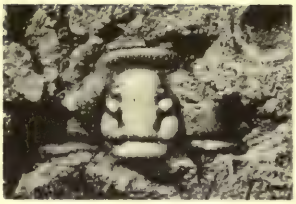
Soudleyan Stage, probably zone of *Broeggerolithus broeggeri*, road-side quarry 150 yards north-east of Chatwall Farm, Chatwall.

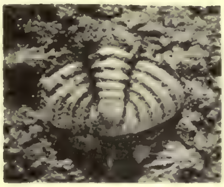
FIG. 16. Internal mould of incomplete cranidium. BM. In. 54320. ×2·5.

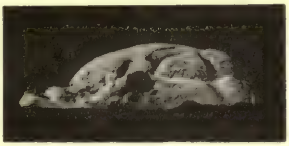
FIGS. 2, 5, 6, 8 and 14 by Mr. E. W. Seavill, remainder by the writer.

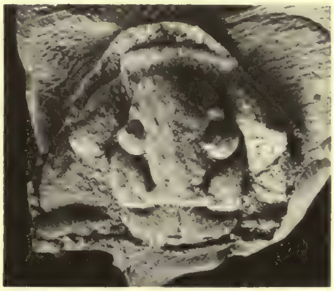

1

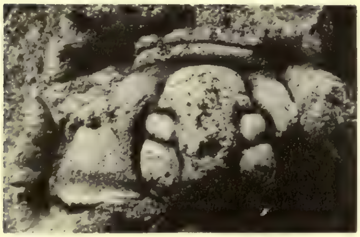

2

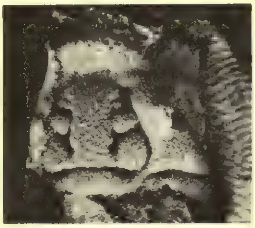

3

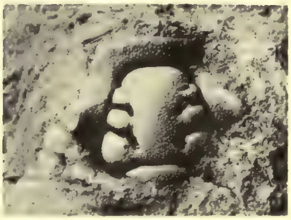

4

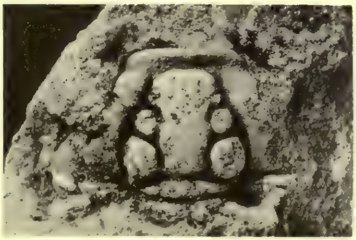

5

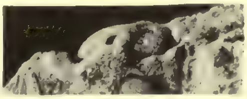

6

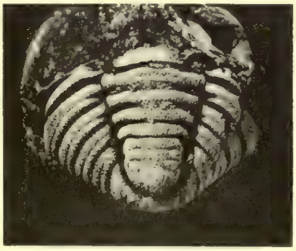

7

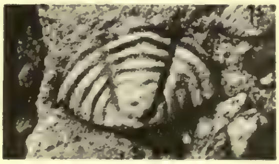

8

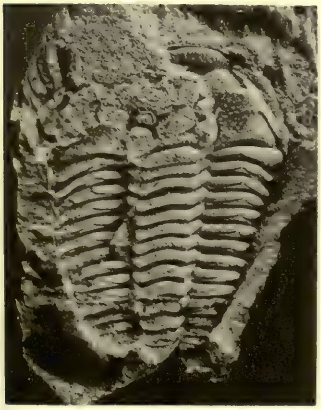

9

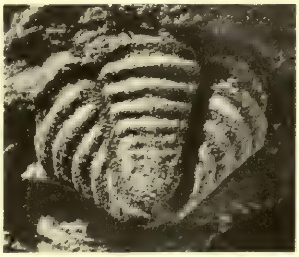

10

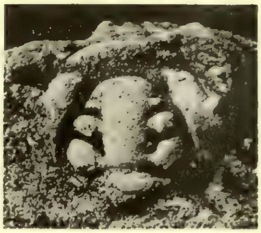

11


12


13


14


15


16

FLEXICALYMENE, FLEXICALYMENE (REACALYMENE)

PLATE 38

Flexicalymene cobboldi sp. nov. . . . . p. 218

Marshbrookian Stage, zone of *Dalmanella unguis*, Marshwood Quarry, ½ mile south of Marshbrook Station.

FIG. 1. Internal mould of cranidium, associated with that of *Otarion* sp. BM. In. 50762. ×2.

Upper Longvillian Substage. zone of *Kjaerina bipartita* (=*Alternata* Limestone), south-eastern side of Horderley–Marshbrook road, 420 yards north-east of Crosspipes, about 2 miles north-east of Horderley Station.

FIG. 3. Holotype, internal mould of cranidium. BM. In. 55448. ×2·3.

Flexicalymene caractaci (Salter) . . . . p. 217

Marshbrookian Stage, zone of *Onniella reuschi*, well-sinking at " first house along road south from The Corner", near Wistanstow.

FIG. 2. Internal mould of incomplete cranidium. BM. In. 52820. ×1·9. Horizon and locality as for Fig. 1.

FIGS. 4, 5. Internal moulds of cranidium, thorax and pygidium, associated on same hand-specimen. Syntypes of *Flexicalymene trigonoceps* Bancroft (1949, pl. 11, fig. 32). BM. In. 42102. Fig. 4, ×2·4 ; Fig. 5, ×2.

Marshbrookian Stage, zone of *Dalmanella wattsi*, " Acton Scott Lodge ", near Acton Scott.

FIG. 6. Lectotype, an internal mould. GSM. 47698. ×1·5. Horizon as for Fig. 2. West side of track in Marsh Wood, just south of the quarry.

FIGS. 8, 11. Internal mould of cranidium illustrating inclined anterior border. BM. In. 50735. Fig. 8, ×2 ; Fig. 11, ×2·5.

Horizon as for Fig. 6, south-eastern side of Horderley road, 520 yards west-south-west of Marshbrook Station.

FIG. 12. Internal mould of incomplete cranidium. BM. In. 55446. ×2.

Onnicalymene laticeps (Bancroft) . . . . p. 224

Actonian Stage, north end of wood west of Rose Villa, Marshbrook.

FIG. 7. Holotype cranidium, an internal mould. BM. In. 42103. ×2. Uppermost Actonian Stage, north bank of River Onny, 62 feet east of junction with Batch Gutter.

FIGS. 10, 14, 15. Uncrushed cranidium with test preserved. BM. In. 50723. ×2·5.

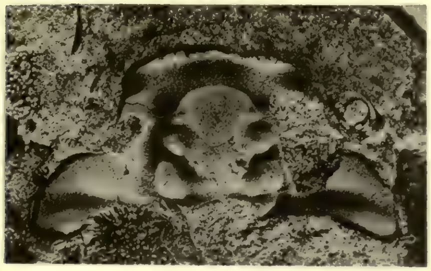
Onnicalymene salteri (Bancroft) . . . . p. 224

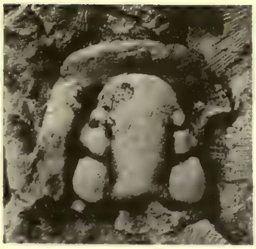
Horizon and locality as for Fig. 7.

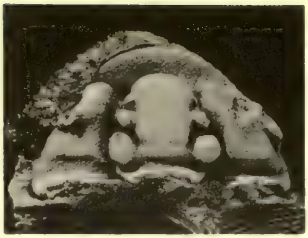
FIG. 9. Holotype cranidium, an internal mould. BM. In. 42100. ×2. Horizon as for Fig. 7, south bank of River Onny, 80 yards west of junction with Batch Gutter.

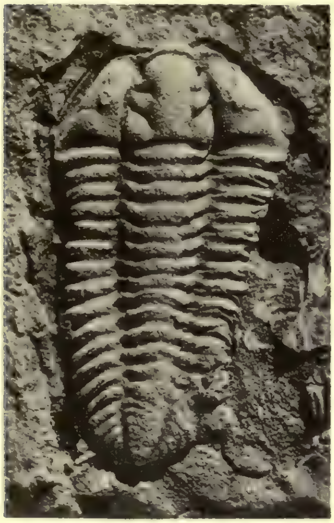
FIG. 13. Incomplete cranidium with test preserved. BM. In. 50736. ×1·8.

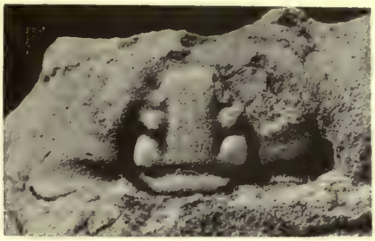
Fig. 1 by Mr. E. W. Seavill, remainder by the writer.

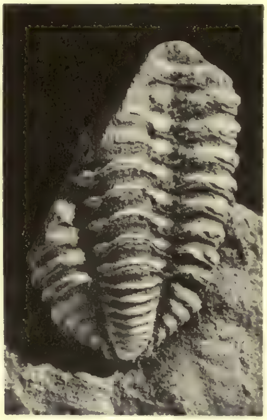

1

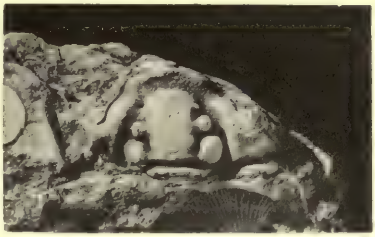

2

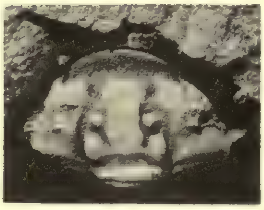

3

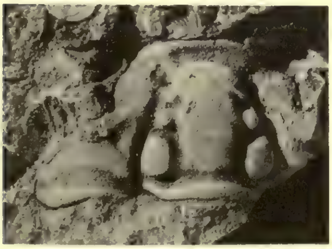

6

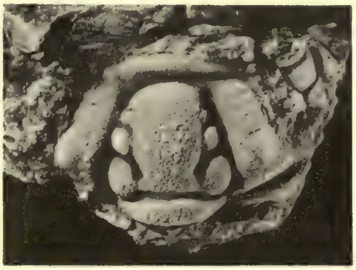

4

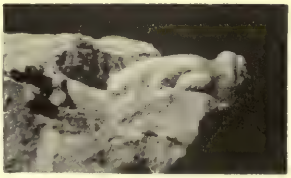

5

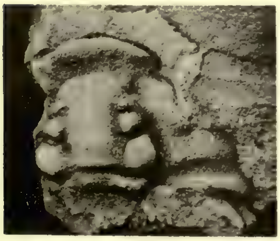

7

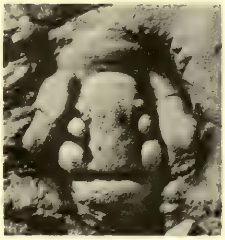

8

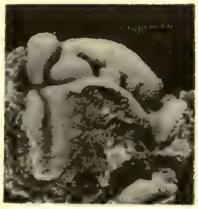

9

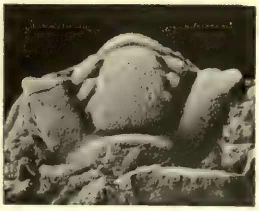

10


11


12


13


14


15

FLEXICALYMENE, ONNICALYMENE

PLATE 39

Gravicalymene praecox (Bancroft) . . . . . p. 225

Harnagian Stage, zone of *Reuscholithus reuschi*, section in old cart-way near south end of Smeathen Wood, near Horderley.

FIG. 1. Slightly crushed internal mould of large cranidium. BM. In. 50523. × 1·8.

FIGS. 3, 9. Internal mould of large, incomplete cranidium showing glabellar outline and form of anterior border and axial furrows. BM. In. 50522. × 2.

FIG. 12. Internal mould of incomplete cranidium showing palpebral lobe and undistorted axial furrows. BM. In. 50657. × 1·8.

FIGS. 13, 14. Holotype, the internal mould of an immature cranidium, the glabella bearing the impression of an ostracod, *Tallinella scripta* (Harper). BM. In. 42090. × 3·5.

Gravicalymene cf. *praecox* (Bancroft) . . . . . p. 225

Onnian Stage, zone of *Onnia gracilis*, north bank of River Onny, 100 yards east of junction with Batch Gutter.

FIG. 4. Cranidium with test preserved. BM. In. 50654. × 1·5.

FIGS. 5, 8. Thorax and pygidium associated with, and believed to belong, to same individual as Fig. 4. BM In. 50655. × 1·5.

Actonian Stage, site of old quarry, Quarry Field, Gretton, near Cardington.

FIG. 7. Internal mould of incomplete cranidium. BM. In. 50648. × 1·5.

Gravicalymene inflata sp. nov. . . . . . p. 227

Horizon and locality as for Fig. 4.

FIG. 6. Holotype, an incomplete cranidium with the test preserved. BM. In. 50653. × 1·5.

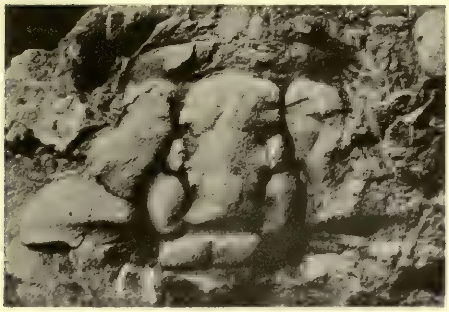
Onnicalymene onniensis (Shirley) . . . . . p. 223

Horizon and locality as for Fig. 4.

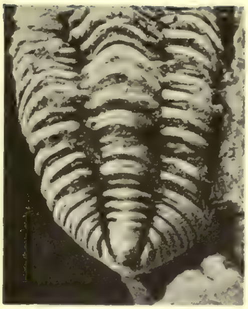
FIG. 2. Thorax and pygidium with test preserved. BM. In. 52092. × 2. Horizon and locality probably as for Fig. 4.

FIGS. 10, 11. Holotype cranidium. GSM. RR 1940. × 2.

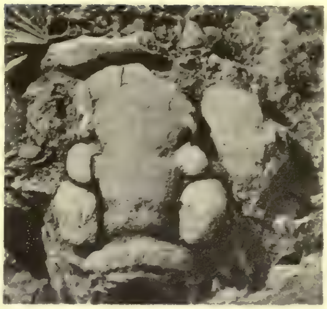
Figs. 4–8 by Mr. E. W. Seavill, remainder by the writer.



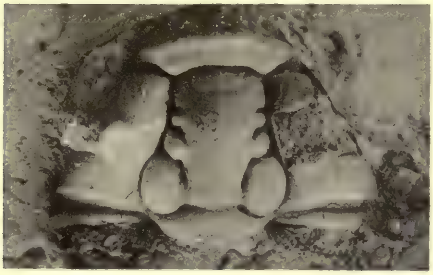
1



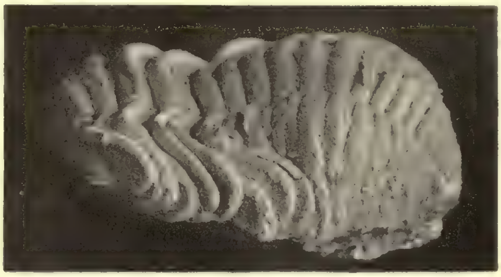
2



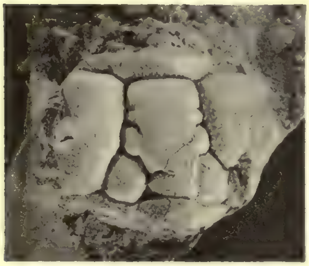
3



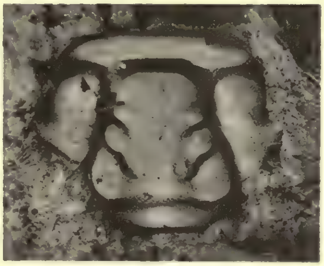
4



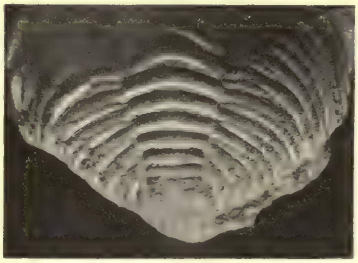
5



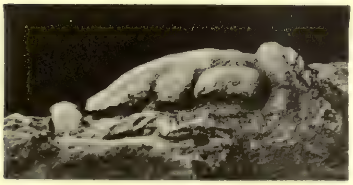
6



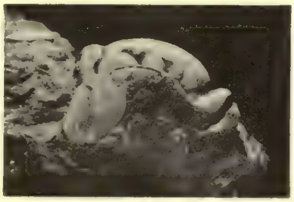
7



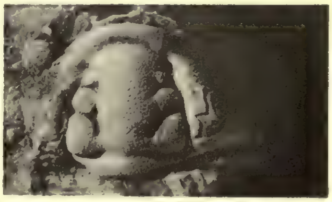
8



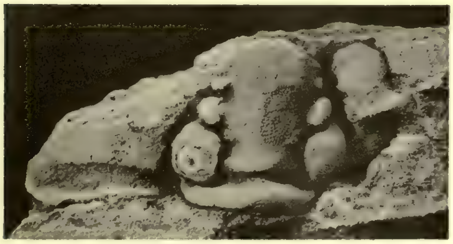
9



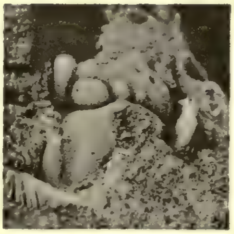
10



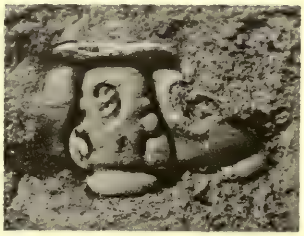
11



12



13



14

GRAVICALYMENE, ONNICALYMENE

PLATE 40

Parabasilicus powisi (Murchison) . . . . . p. 229

Costonian Stage, probably zone of *Harknessella subquadrata*, old quarry just west of Round Nursery, south-east of Harnage Grange.

FIG. 1. Internal mould of pygidium and fragment of thorax. BM. In. 52197. ×1·3.

Soudleyan Stage, zone of *Broeggerolithus broeggeri*, exposure behind Glenburrell farmhouse, Horderley.

FIG. 3. Internal mould of pygidium and thorax. BM. In. 52186. ×1·1.

Harnagian Stage, zone of *Reuscholithus reuschi*, south bank of Coundmoor Brook, 1340 yards south-west of Harnage Farm, Harnage.

FIG. 4. Internal mould of cranidium with fragments of test, showing course of facial suture. BM. In. 54237. ×1·5.

FIG. 5. Internal mould of slightly distorted pygidium showing anterolateral facets. BM. In. 54238. ×2·2.

Parabasilicus powisi (Murchison) ? . . . . . p. 231

Middle Costonian Stage, *Harknessella* Beds, north side of cartway 50 yards east of Coston Farmhouse, 1 mile east of Clunbury.

FIG. 2. Internal mould of hypostoma lacking anterior wings. BM. In. 50621. ×1·6.

Parabasilicus ? sp. . . . . . . p. 232

Lower Longvillian Substage, zone of *Dalmanella indica* and *D. lepta*, top of western end of Rookery Wood, south-east of Horderley.

FIG. 6. Internal mould of pygidium. BM. In. 50741. ×1·5.

Flexicalymene (*Reacalymene*) *horderleyensis* sp. nov. . . p. 221

Horizon as for Fig. 6, old quarry just west of western end of Rookery Wood, south-east of Horderley.

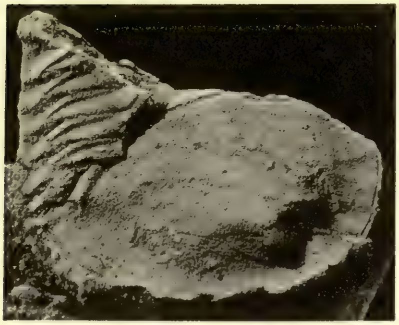
FIGS. 7, 8. Internal mould of incomplete cranidium. BM. In. 52103. ×2.

Onnicalymene onniensis (Shirley) . . . . . p. 223

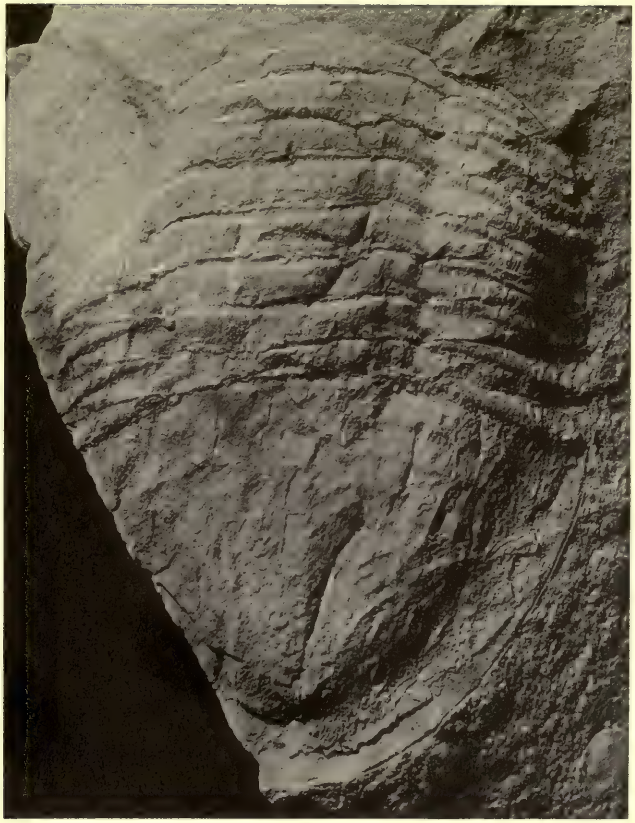
Onnian Stage, zone of *Onnia superba*, north bank of River Onny 720 yards west-south-west of Wistanstow Church.

FIG. 9. Internal mould of cranidium. BM. In. 50711. ×2.

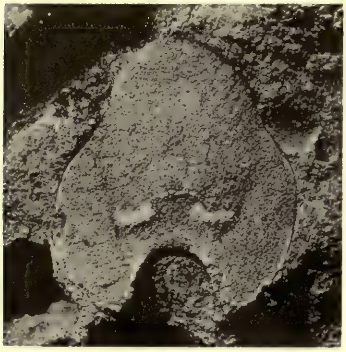
Fig. 9 by Mr. E. W. Seavill, remainder by the writer.



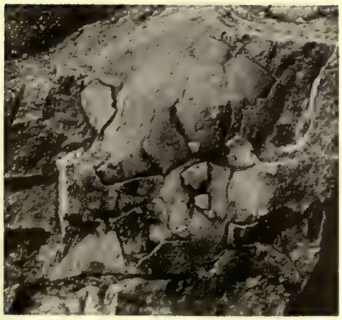
1



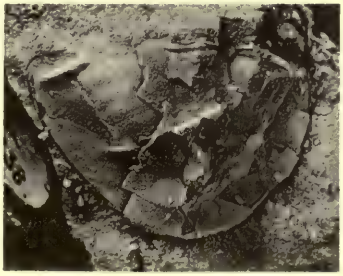
3



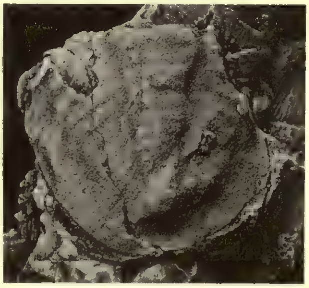
2



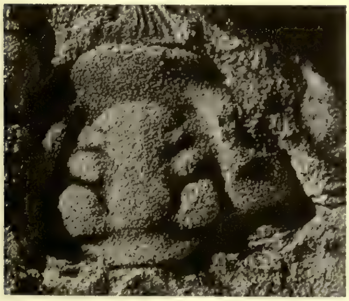
4



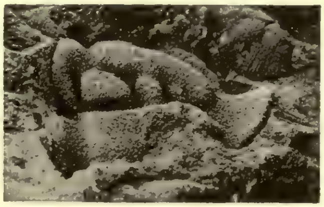
5



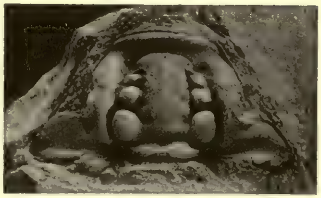
6



7



8



9

FLEXICALYMENE (REACALYMENE) ONNICALYMENE PARABASILICUS

PLATE 41

Parabasilicus powisi (Murchison) . . . . . p. 229

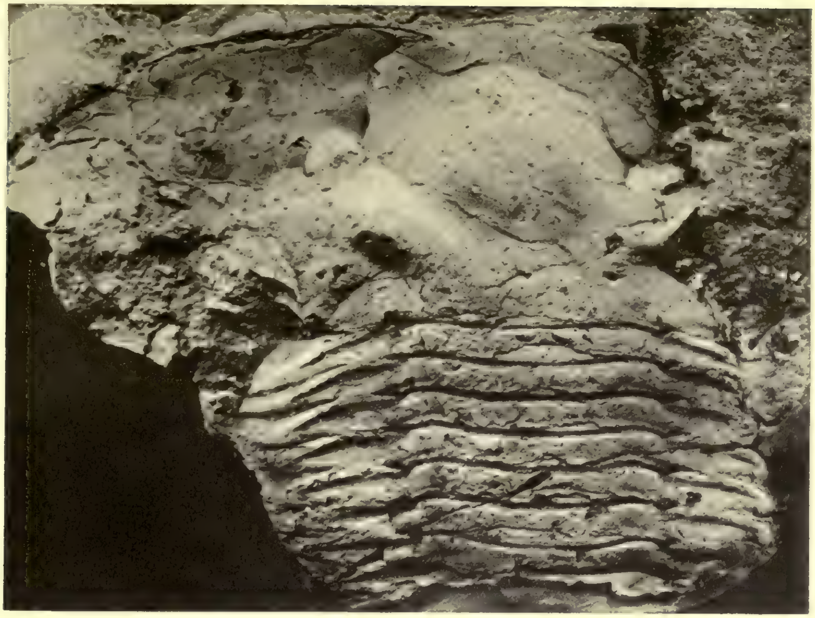
Soudleyan Stage, zone of *Broeggerolithus broeggeri*, eastern bank of Habberley Brook, 500 yards north of The Lyd Hole, near Pontesford, Shropshire.

FIG. 1. Internal mould of cranidium, left librigena (displaced), and thorax. BM. In. 54305. ×1·1.

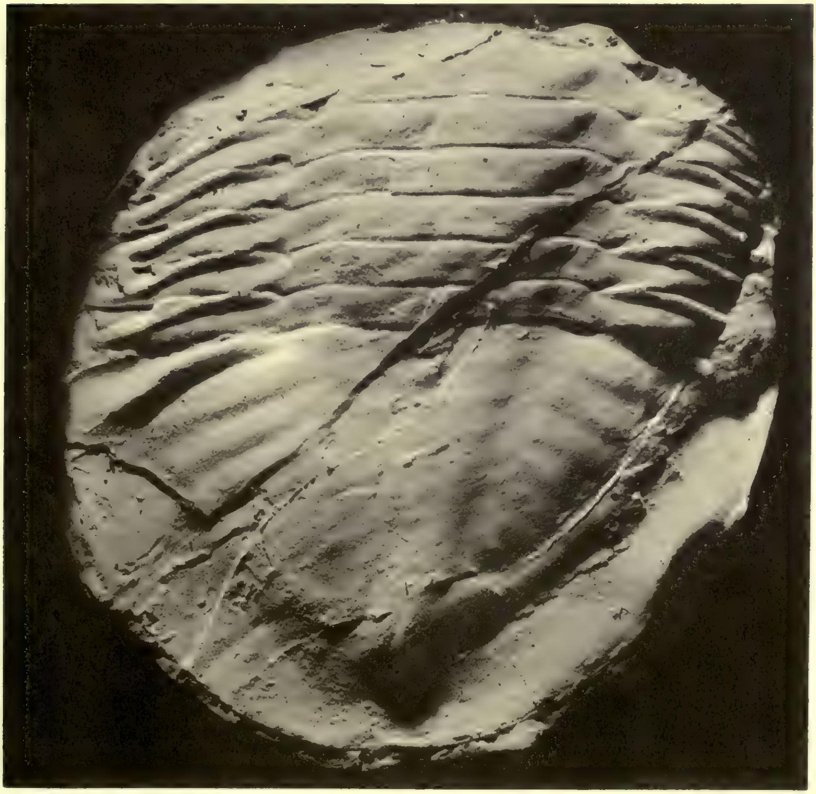
Probably Harnagian Stage, Bron-y-buckley Wood (=Trilobite Dingle), Welshpool, Montgomeryshire.

FIG. 2. Vinyl plastic cast of lectotype, an external mould of pygidium and incomplete thorax GSM. 6841. ×1·1.

Fig. 1 by the writer, Fig. 2 by Mr. J. Brown.



1



2

PARABASILICUS

PLATE 42

Parabasilicus ? ***marstoni*** (Salter) . . . . p. 231

Horizon probably Smeathen Wood Beds, Harnagian Stage *pars*, of the Horderley district. Exact locality unknown.

FIGS. 1, 6. Syntype, internal mould of an almost complete dorsal exoskeleton with damaged cephalon. GSM. 12817. ×4. Fidg. Salter, 1866, pl. 23, figs. 1, 1*a*.

FIG. 8. Syntype, internal part external mould of right librigena. GSM. 12818. ×2·5. Figd. Salter, 1865, pl. 23, fig. 1*b*.

Parabasilicus ? sp. . . . . . p. 232

Probably from the Horderley Sandstone, Lower Longvillian Substage, of the Horderley district.

FIG. 2. Internal mould of hypostoma. GSM. 12830. ×2. Figd. Salter, 1866, pl. 23, fig. 6. Lower Longvillian Substage, zone of *Dalmanella horderleyensis*, quarry by north side of road, 300 yards south-east of Glenburrell Farm, Horderley.

FIG. 5. Internal mould of pygidium. BM. In. 51459. ×2.

Parabasilicus powisi (Murchison) . . . . p. 229

Harnagian Stage, zone of *Reuscholithus reuschi*, section in old cart-way near southern end of Smeathen Wood, near Horderley.

FIG. 9. Latex cast from external mould of frontal portion of cranidium. BM. In. 51462. ×2.

Illaenus cf. *fallax* Holm . . . . . p. 233

Onnian Stage, zone of *Onnia* ? *cobboldi*, north bank of River Onny, about 70 yards east of junction with Batch Gutter.

FIG. 3. Internal mould of pygidium. BM. In. 50760. ×1·9. Onnian Stage, zone of *Onnia gracilis*, north bank of River Onny, 100 yards east of junction with Batch Gutter.

FIG. 4. Internal mould of pygidium. BM. In. 50515. ×1·9.

FIG. 12. Cranidium with most of test preserved. BM. In. 50759. ×1·3.

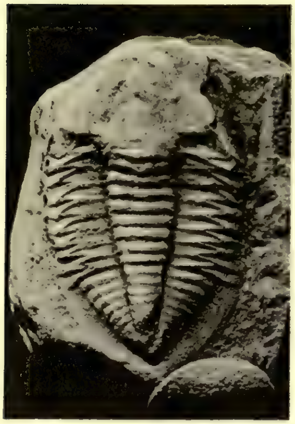
Illaenus sp. . . . . p. 233

Actonian Stage, site of old quarry, Quarry Field, Gretton, near Cardington.

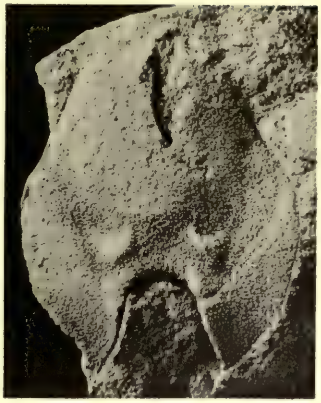
FIGS. 7, 10. Internal mould of cranidium. BM. In. 50576. ×1·6.

FIG. 11. Internal mould of immature cranidium. BM. In. 50755. ×2·3.

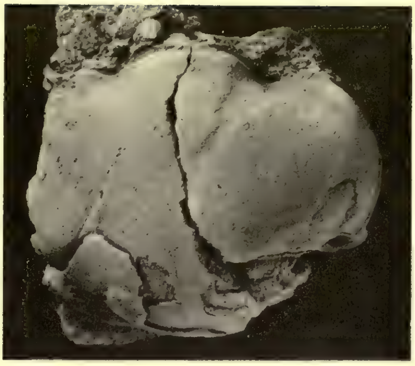
Figs. 7, 10 by Mr. E. W. Seavill, remainder by the writer.



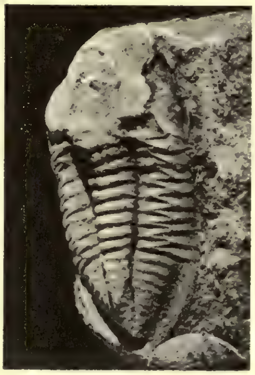
1



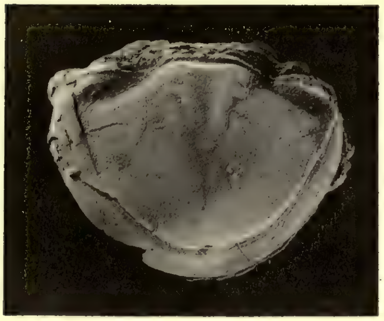
2



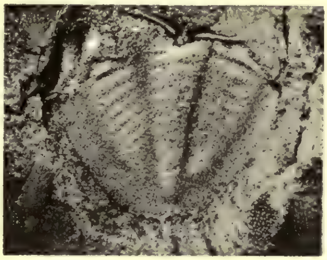
3



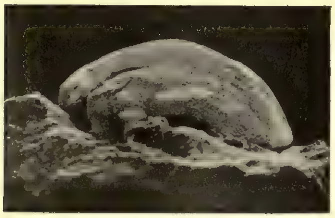
6



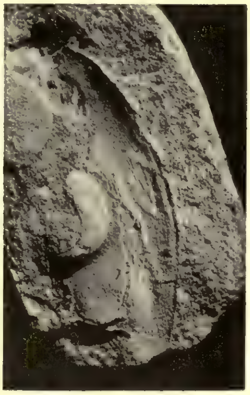
4



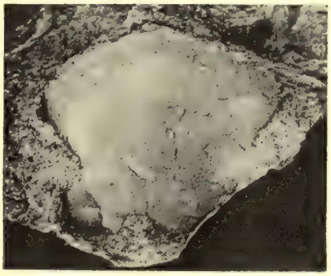
5



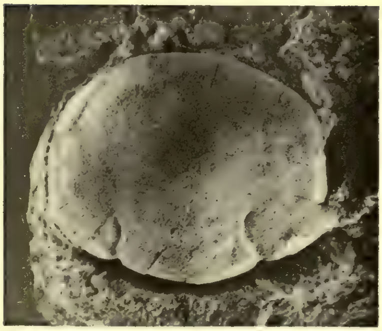
7



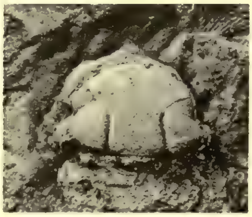
8



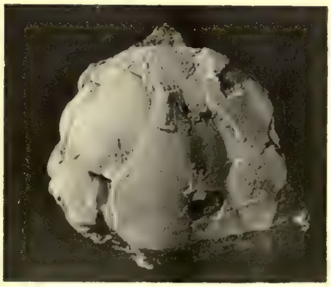
9



10



11



12

PARABASILICUS, ILLAENUS

PLATE 43

Metopolichas ? sp. . . . . . . p. 234

Costonian Stage, zone of *Harknessella subquadrata*, old quarry by south-eastern side of brook, 1500 yards south-west of Harnage Farm, Harnage.

FIGS. 3, 6, 7. Internal mould of incomplete, slightly distorted cranidium. BM. In. 46455. Figs. 3, 6, ×1·4; Fig. 7, ×2.

Costonian Stage, zone of *Costonia ultima*, old quarry 650 yards west of Woolston House, Woolston.

FIG. 4. Internal mould of fragmentary cranidium. GSM. RR 2140. ×2.

Platylichas laxatus (M'Coy) . . . . . p. 235

Actonian Stage, site of old quarry, Quarry Field, Gretton, near Cardington.

FIG. 1. Latex cast from external mould of large pygidium. BM. In. 49558. ×1·4.

FIG. 8. Internal mould of incomplete cranidium. BM. In. 50749. ×1·5.

FIG. 12. Internal mould of hypostoma. BM. In. 50524. ×1·7.

Horizon as for Fig. 1, south bank of River Onny, 80 yards west of junction with Batch Gutter.

FIG. 2. Incomplete cranidium showing surface of test. BM. In. 50747. ×2.

Horizon as for Fig. 1, old quarry 1400 feet west-south-west of St. Margaret's Church, Acton Scott.

FIG. 5. Internal and partly external mould of pygidium, showing impression of terrace-lines on doublure. BM. In 50754. ×2·4.

Caradoc Series, Slieveroe, Rathdrum, Ireland.

FIG. 10. Holotype, a fragmentary cranidium. National Museum of Ireland Collection. ×2.

Horizon as for Fig. 1, locality as for Fig. 2.

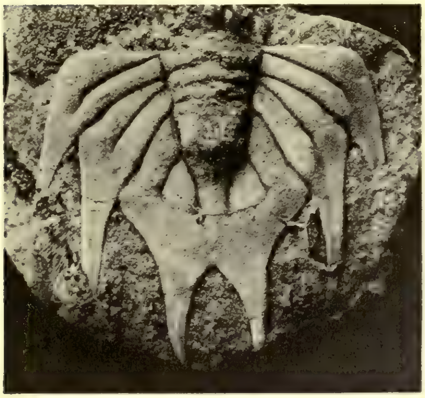
FIG. 11. Almost complete cranidium. BM. In. 46440. ×1·4.

Platylichas sp. . . . . . . p. 236

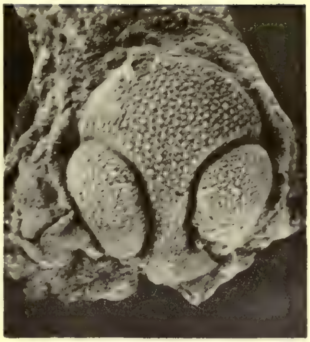
FIG. 9. Internal mould of pygidium, figured by M'Coy, 1846, pl. 4, fig. 14, as *Calymene forcipata*. National Museum of Ireland Collection. ×1·75.

Caradoc Series, Ballygarvan Bridge, New Ross, Ireland.

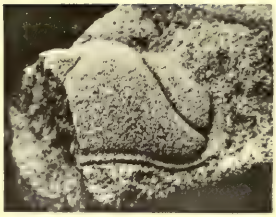
Figs. 2, 9, 10 by Mr. E. W. Seavill, remainder by the writer.



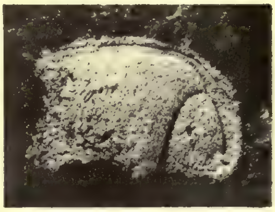
1



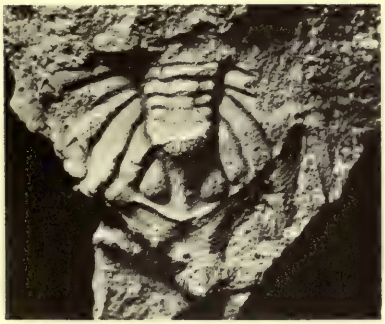
2



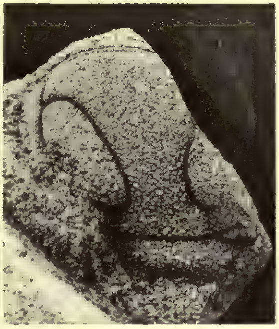
3



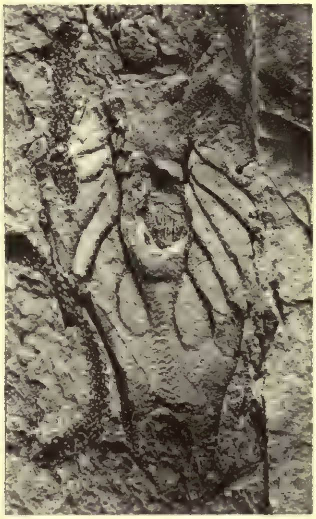
4



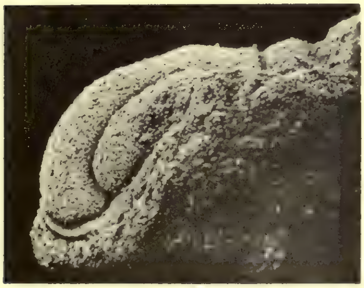
5



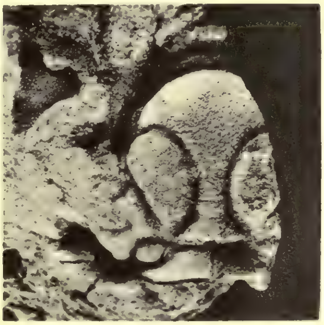
6



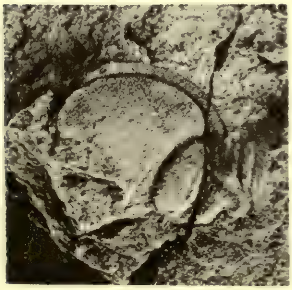
9



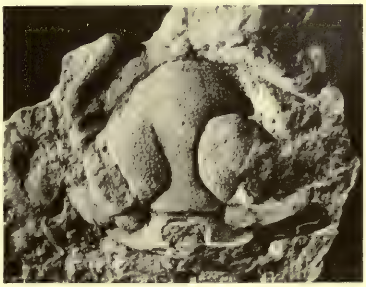
7



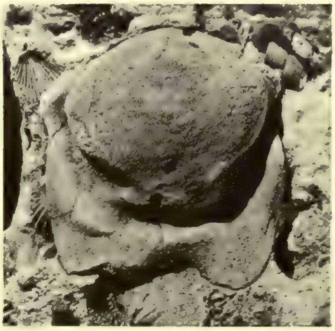
8



10



11



12

LICHAS ?, PLATYLICHAS

PLATE 44

Primaspis harnagensis (Bancroft) . . . . . p. 237

Harnagian Stage, zone of *Reuscholithus reuschi*, section in old cart-way near southern end of Smeathen Wood, near Horderley.

FIG. 1. Internal mould of cranidium. BM. In. 50802. × 9.

FIG. 6. Paratype pygidium, an internal mould. BM. In. 42087. × 2·5.

FIG. 8. Latex cast from external mould of librigena. BM. In. 50803. × 4.

Horizon as for Fig. 1. By north bank of Coundmoor Brook, 1300 yards south-west of Harnage Farm, Harnage.

FIG. 4. Internal mould of cranidium, slightly distorted. BM. In. 52829. × 8.

Primaspis caractaci (Salter) . . . . . p. 239

Actonian Stage, site of old quarry, Quarry Field, Gretton, near Cardington.

FIG. 3. Internal mould of cranidium. BM. In 50805. × 4.

FIG. 9. Syntype thorax. GSM. 5214. × 5.

FIG. 13. Syntype, internal mould of almost complete dorsal exoskeleton. GSM. 35473. × 4.

Horizon as for Fig. 3. Bank of stream by east side of bridge *c.* 1000 feet west-south-west of Hatton.

FIG. 7. Two incomplete cranidia with test preserved. BM. In. 50510. × 3·5. Horizon as for Fig. 3. Old quarry by road almost opposite Church Farm, Acton Scott.

FIG. 11. Latex cast from external mould of librigena. BM. In. 50801. × 4.

Marshbrookian Stage, zone of *Onniella reuschi*, west side of track just south of quarry in Marsh Wood, near Marshbrook.

FIG. 14. Poorly-preserved librigena. BM. In. 50799. × 3.

Triarthrus cf. *linnarssoni* Thorslund . . . . p. 241

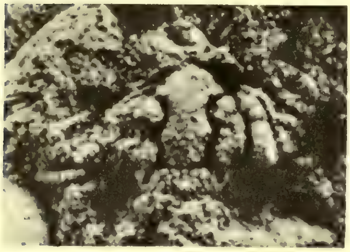
Onnian Stage, zone of *Onnia superba*, north bank of River Onny, 720 yards west-south-west of Wistanstow Church.

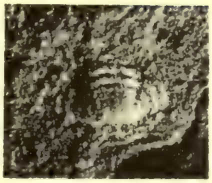
FIG. 2. Internal mould of immature pygidium. BM. In. 49320. × 10.

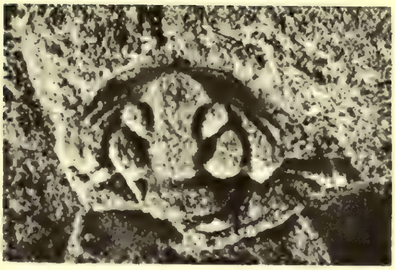
FIG. 5. Incomplete immature cranidium showing position of palpebral lobe. BM. In. 51528. × 5·5.

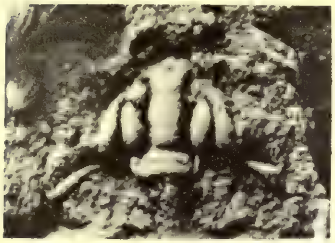
FIGS. 10, 12. Internal mould of cranidium. Shrewsbury Museum 374. × 4.

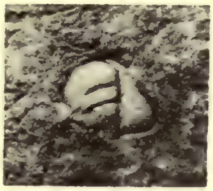
Figs. 1, 3, 8, 10–12 by Mr. E. W. Seavill, Fig. 2 by Mr. J. Brown, remainder by the writer.

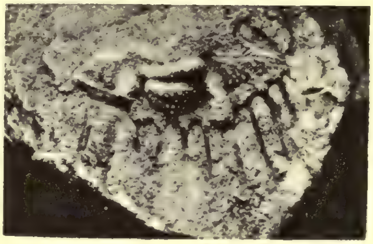

1

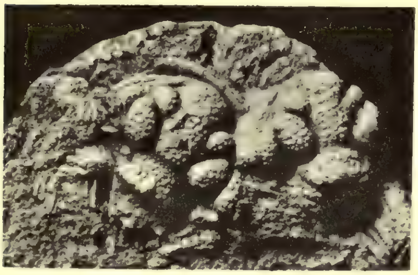

2

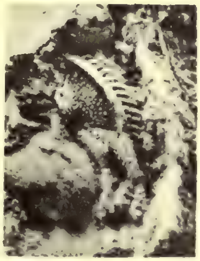

3

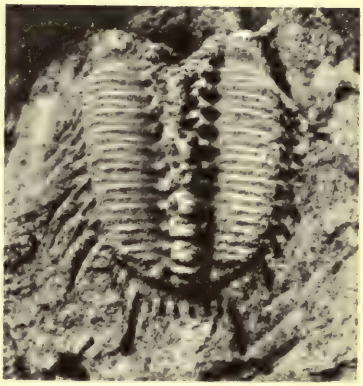

4

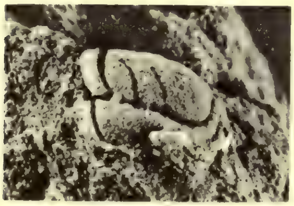

5

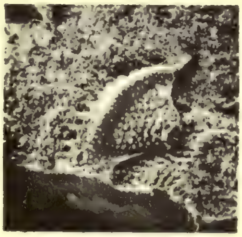

6

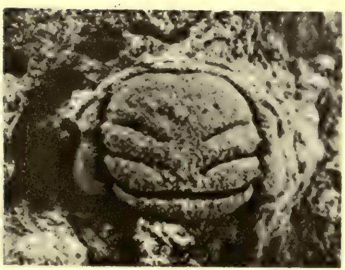

7

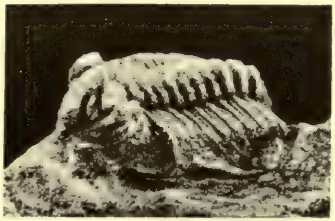

8

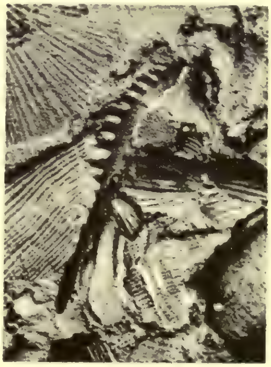

9


10


11


12


13


14

PRIMASPIS, TRIARTHRUS

PLATE 45

Otarion sp. . . . . p. 242

Marshbrookian Stage, zone of *Dalmanella unguis*, west side of track, 70 yards south of entrance to quarry, Marsh Wood, near Marshbrook.

FIG. 1. Latex cast of cranidium. BM. In. 50618. ×4·5.

Remopleurella burmeisteri (Bancroft) . . . . . p. 250

Onnian Stage, zone of *Onnia superba*, north bank of River Onny, 720 yards west-south-west of Wistanstow Church.

FIG. 2. Internal mould of hypostoma. BM. In. 56800*a*. ×7.

Proetidella fearnsidesi Bancroft . . . . . p. 243

Harnagian Stage, zone of *Reuscholithus reuschi*, section in old cartway near southern end of Smeathen Wood, near Horderley.

FIG. 3. Latex cast from the holotype, an external mould. BM. In. 42083. ×3·4.

FIG. 8. Internal mould of immature thorax. BM. In. 51454. ×2·9.

FIGS. 12, 14. Internal moulds of cranidia, showing variation in outline of glabella. Fig. 12, BM. In. 55449, ×3·4. Fig. 14, BM. In. 51522, ×3·25.

Horizon as for Fig. 3. Exposure in field, 550 yards north-west of Woolston House, Woolston.

FIG. 4. Internal mould of cephalon showing palpebral lobe and facial suture. BM. In. 50616. ×3.

FIG. 5. Internal mould of immature cranidium. BM. In. 51455. ×3·5.

Costonian Stage, zone of *Harknessella subquadrata*, old quarry just west of western end of Round Nursery, south of Harnage Grange.

FIGS. 6, 7. Internal mould of nearly whole dorsal exoskeleton. BM. In. 51152. ×3.

Proetidella cf. *fearnsidesi* Bancroft . . . . p. 245

Soudleyan Stage, ? zone of *Broeggerolithus broeggeri*, road-side quarry 150 yards north-east of Chatwall Farm, Chatwall.

FIG. 9. Internal mould of cranidium. BM. In. 34326. ×4.

FIG. 11. Internal mould of left librigena. BM. In. 34325. ×3·25.

Soudleyan Stage, zone of *Broeggerolithus soudleyensis*, road-side quarry 100 yards south-east of Glenburrell Farm, Horderley.

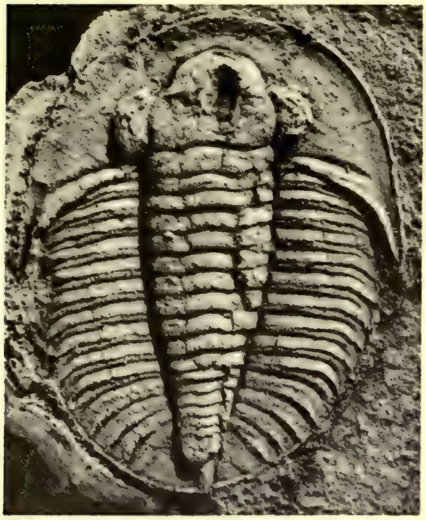
FIG. 10. Internal mould of cranidium. BM. In. 51456. ×2.

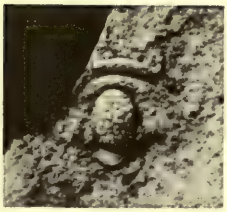
Proetidella ? sp. . . . . . . p. 246

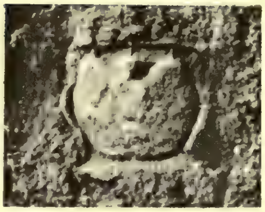
Marshbrookian Stage, zone of *Dalmanella unguis*, stream bank about 350 yards north-west of road bridge, 350 yards south-west of Hatton, near Acton Scott.

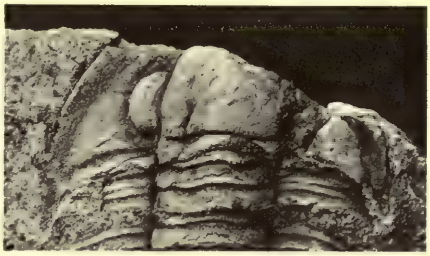
FIG. 13. Internal mould of cranidium. BM. In. 50617. ×4.

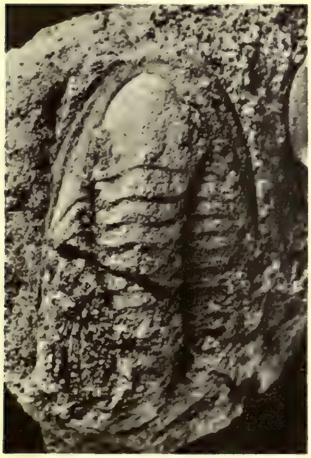
Photographs by the writer.

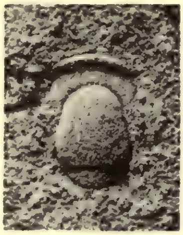

3

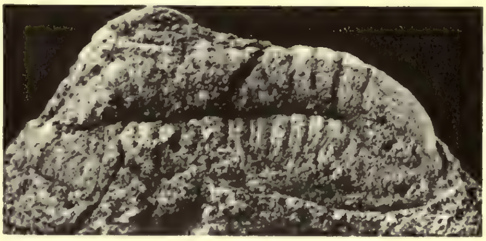

1

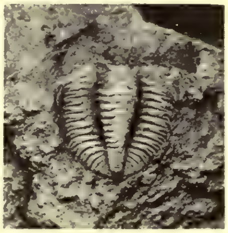

2

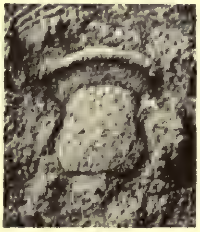

4

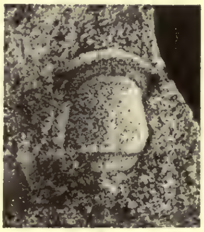

7

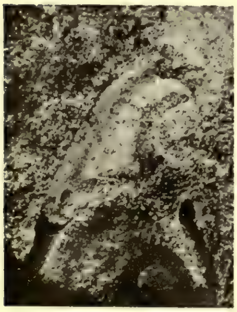

5

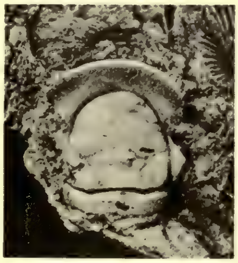

6

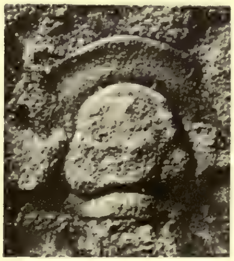

8

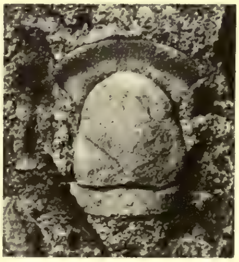

9


10


11


12


13


14

OTARION, PROETIDELLA, REMOPLEURELLA

PLATE 46

Remopleurides warburgae sp. nov. . . . . . p. 246

Highest beds of Actonian Stage, north bank of River Onny, 30 yards east of junction with Batch Gutter.

FIGS. 1, 2. Holotype cranidium with test preserved. BM. In. 49751. ×2·5.

Remopleurides latus Olin *onniensis* subsp. nov. . . . p. 247

Horizon and locality as for Fig. 1.

FIGS. 4, 5. Holotype cranidium. BM. In. 49750. ×2·5.

Remopleurides sp. . . . . . . p. 248

Horizon and locality as for Fig. 1.

FIG. 3. Almost complete left librigena. BM. In. 49752. ×2·5.

FIG. 7. Incomplete thorax showing serrated axial rings and shape of pleurae. BM. In. 49753. ×3.

Remopleurella burmeisteri (Bancroft) . . . . p. 250

Onnian Stage, zone of *Onnia superba*, north bank of River Onny, 720 yards west-south-west of Wistanstow Church.

FIG. 6. Paratype, internal mould of librigena. BM. In. 42098. ×2·5.

FIGS. 8, 12. Paratype, incomplete, disarticulated exoskeleton preserved as internal mould. BM. In. 49561. Fig. 8, ×2·5. Fig. 12, hypostoma, In. 49561*a*, ×6.

FIG. 9. Internal mould of cranidium showing palpebral lobes. BM. In. 49748. ×5·25.

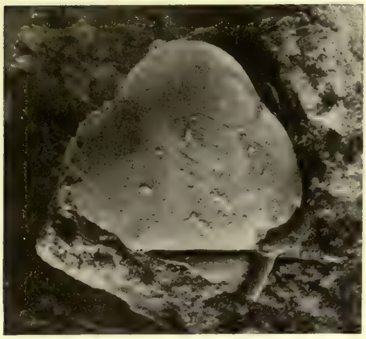
FIG. 11. Lectotype, internal mould of cranidium. BM. In. 42106. ×2·75.

Eobronteus ? sp. . . . . . . p. 251

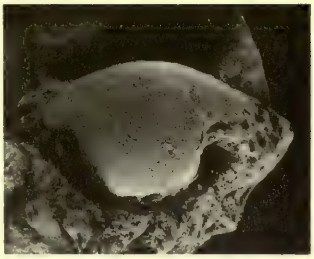
Horizon and locality as for Fig. 6.

FIG. 10. Internal mould of incomplete dorsal exoskeleton. Sedg. Mus. A. 43833. ×2.

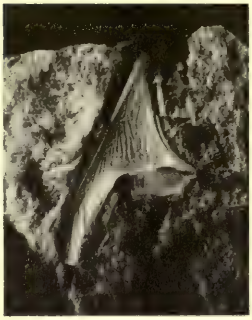
FIGS. 1-5, by Mr. E. W. Seavill, Fig. 10 by Mr. J. Brown, remainder by the writer.



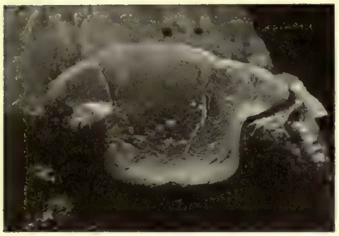
1



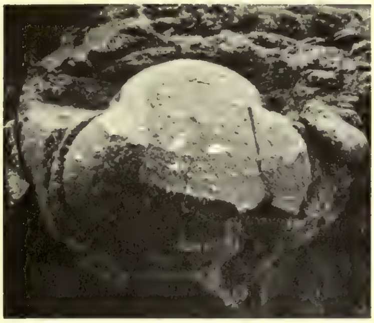
2



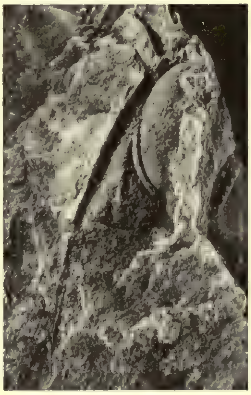
3



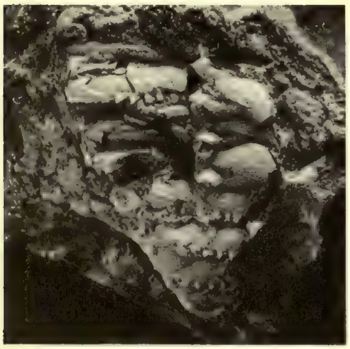
4



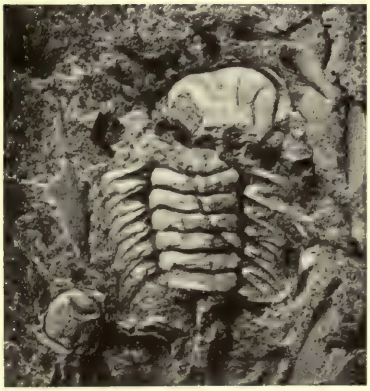
5



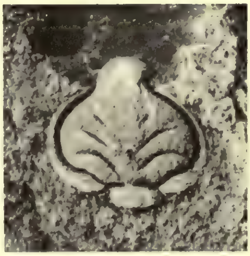
6



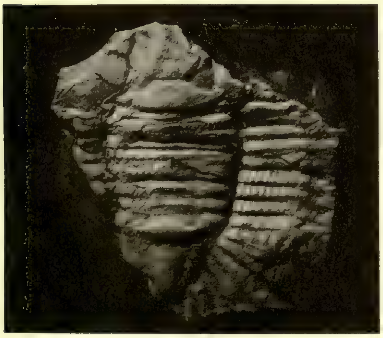
7



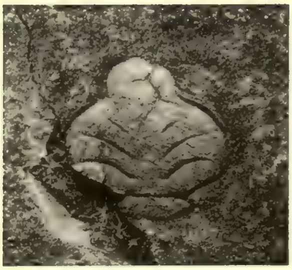
8



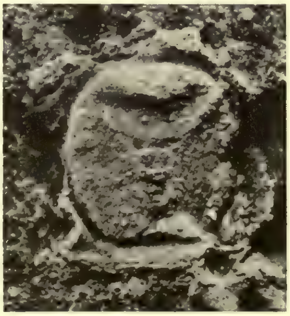
9



10



11



12

EOBRONTEUS?, REMOPLEURELLA, REMOPLEURIDES

[illegible]

PRINTED IN GREAT BRITAIN BY
ADLARD AND SON, LIMITED,
BARTHOLOMEW PRESS, DORKING

THE GASTROPOD GENUS *THATCHERIA* AND ITS RELATIONSHIPS

A. J. CHARIG

BRITISH MUSEUM
17 JUL 1963
NATURAL HISTORY

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 7 No. 9
LONDON: 1963

THE GASTROPOD GENUS *THATCHERIA* AND ITS RELATIONSHIPS

BY

ALAN JACK CHARIG

17 JUL 1963

Pp. 255–297 ; *Plate* 47 ; 10 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 7 No. 9
LONDON : 1963

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

This paper is Vol. 7, No. 9 of the Geological (Palaeontological) series.

© Trustees of the British Museum 1963

PRINTED BY ORDER OF THE TRUSTEES OF
THE BRITISH MUSEUM

Issued July 1963 *Price Sixteen Shillings*

THE GASTROPOD GENUS *THATCHERIA* AND ITS RELATIONSHIPS

By A. J. CHARIG

CONTENTS

		Page
I.	INTRODUCTION	258
II.	HISTORY OF *Thatcheria* AND OF THE VIEWS ON ITS RELATIONSHIPS	258
III.	NOTES ON *Thatcheria mirabilis* ANGAS	268
	Identification of the holotype	268
	Additional material in the British Museum (Natural History)	269
	Supplementary description	269
IV.	NOTES ON *Clinura*	271
	Material studied	271
	Posterior sinus	272
	Protoconch	274
	Transverse sculpture	274
V.	NOTES ON *Waitara liratula* POWELL	275
	Protoconch	275
	Transverse sculpture	276
VI.	SYSTEMATICS	276
	General principles	276
	The *Clinura–Thatcheria* group	278
	Division into genera	281
	Interspecific differentiation in *Thatcheria*	283
	Evolution in the *Clinura–Thatcheria* group	286
	Systematic position of the *Clinura–Thatcheria* group	288
	Formal classification	291
VII.	A NEW SPECIES OF *Thatcheria* FROM THE PLIOCENE OF FIJI	292
VIII.	ACKNOWLEDGMENTS	294
IX.	REFERENCES	295

SYNOPSIS

The literature on the subject is reviewed with particular reference to the systematics of the genera concerned.

A Recent gastropod shell, Brit. Mus. (Nat. Hist.) no. 1960.154, is identified as the holotype of the type-species of *Thatcheria* (*T. mirabilis* from off Japan). The description is amplified.

The form of the posterior sinus in *Clinura* has been generally misunderstood. The protoconch, hitherto unknown in the genus, is described in the type-species and in one other. The protoconch of *Waitara liratula* is re-examined.

The systematics of the genera concerned are reconsidered. *Clinura* is restricted to a few species from the Neogene of Europe and of the Western Pacific. *Clinura*, *Waitara* and *Thatcheria* are closely related to each other but not to *Surculites*. Fourteen species in those three genera are reclassified into two genera, *Clinura* (mainly Miocene) and *Thatcheria* (Upper Miocene to Recent, mainly Pliocene) ; *Thatcheria* is confined to the Western Pacific. The two genera constitute a sub-family of the Turridae, the Thatcheriinae, which has affinities with the Daphnellinae.

Thatcheria vitiensis sp. nov. is described and figured from one specimen of probable Lower Pliocene age from Fiji.

I. INTRODUCTION

THE discovery of a new fossil gastropod which resembles *Thatcheria* and *Waitara* has led to a re-examination of this little-known group of genera. The conclusions reached have been based upon all the relevant literature and upon a few shell characters hitherto unknown or imperfectly understood.

Some of the earlier descriptions and illustrations of the gastropods in question were inadequate or misleading (especially with reference to the form of the posterior sinus and of the consequent growth-lines, the taxonomic significance of which had not then been appreciated). One drawing in particular, upon which some later workers relied for their knowledge of a type-species, is also quite different in that respect from the less accessible description and figures of the original author. The extreme scarcity of actual material obliged most later workers to rely very largely upon these earlier descriptions and figures, and misunderstandings therefore arose. Language difficulties appear to have exacerbated the situation. Finally, it is also evident that certain important works on the *Thatcheria-Waitara* group of gastropods were written in ignorance of the existence of some of the others. But this was sometimes unavoidable ; for example, two of the most important were written and published at about the same time during the Second World War, one in New Zealand and the other in the German-occupied Netherlands.

Thus, while the known members of the group are few in number, both as species and as individuals, their systematics are confused. Although only two named species (*Thatcheria mirabilis* and *T. gradata*) have been referred to the genus *Thatcheria* itself, those two species have already been placed by various authors in ten different prosobranch taxa of the genus-group (excluding synonyms). They have been considered, at least implicitly, as belonging to eight different prosobranch families, five of which possess alternative names. Indeed, one author alone (Wenz, 1943) has referred the two forms concerned and the closely related genus *Waitara* to three separate families. It has also been suggested that *T. mirabilis* is an opisthobranch, and elsewhere stated quite dogmatically that it is a " scalariform monstrosity ". In all, in connexion with *T. mirabilis* and *T. gradata*, sixteen family names are involved.

However, it is now generally accepted that these molluscs are so closely related as to form a natural group. The group might be either a sub-family within the Turridae or, as has been suggested, a separate family with strong affinities therewith. The status and relationships of the group require careful consideration, and the systematics within the group are in need of revision.

II. HISTORY OF *THATCHERIA* AND OF THE VIEWS ON ITS RELATIONSHIPS

Thatcheria mirabilis gen. et sp. nov. was described and figured by Angas (1877 : 529, pl. 54, figs. 1*a*, *b*). His material consisted of one fairly large pagodiform shell believed to be unique ; it had been brought from Japan not long before by Mr. Charles Thatcher, and its occurrence could be localised no more accurately than " Seas of Japan ". No indication was given as to where the shell was deposited.

Of its systematic position, Angas wrote : " Without a knowledge of the operculum, its exact generic position cannot be determined ; but at present I regard it as belonging to the subfamily Fusinae " (i.e. in the family then called Fusidae, now either called Fusinidae or regarded as part of the Fasciolariidae).

The next reference to the specimen is by G. B. Sowerby (1880 : 105, pl. 422, figs. 45, 46), who wrote that it " has been thought to exhibit, in the arched sinus of the outer lip above the angle, a peculiarity of generic value." He nevertheless referred the species to the genus *Pyrula*. (The " *Thesaurus Conchyliorum* " does not place genera in families, but the genus *Pyrula* Lamarck 1799, which should be replaced by the older synonym *Ficus* Röding 1798, is now referred to its own family Pyrulidae or Ficidae). Sowerby also considered Angas' type to be immature, and mentioned that it was " in the collection of Mrs. Deburch ".

Tryon (1881 : 98, 112, pl. 44, figs. 238, 239) retained Angas' genus *Thatcheria* and referred it to the sub-family Melongeninae or Melongeniinae of the family Buccinidae ; but his arrangement might indicate that he considered *Thatcheria* to be synonymous with the older genus *Hemifusus* Swainson. Further, he opined that Angas' specimen did not represent the normal form of the genus, for he wrote " That this shell is a scalariform monstrosity cannot be doubted ". Later (1883 : 135, pl. 49, fig. 5) he gave an exact repetition of his earlier text.

Fischer (1884 : 623) reported Tryon as considering *Thatcheria* to be a scalariform monstrosity of " *Semifusus* Swainson em. 1840 (*Hemifusus*)." In fact, *Semifusus* Agassiz 1846 is an invalid emendation of *Hemifusus* Swainson 1840. Fischer placed this genus in the sub-family Melongeninae of the family Turbinellidae (sometimes called Xancidae or Vasidae) ; the sub-family in question is now generally regarded as a separate family, the Melongenidae.

Cossmann was at first (1889 : 162) unable to agree with Tryon on this matter ; the form of the sinus, as indicated by the growth-lines on the ramp, led him to believe that *Thatcheria* could well be a junior synonym of *Mayeria* Bellardi 1873. *Mayeria*, in any case, seemed to be close to " *Semifusus* ", for Cossmann placed them both together (in the same family and sub-family as Fischer had done). Later, however (1901 : 62, 93, 94), Cossmann decided that the canal of *Thatcheria* distinguished it from *Mayeria*, and that Tryon was correct after all in supposing *Thatcheria* to be but a monstrosity of " *Semifusus* ".

Meanwhile Pilsbry (1895 : 28) had reverted to Tryon's classification and had listed *Thatcheria mirabilis* in the Buccinidae.

No further mention of *Thatcheria* has been discovered earlier than Tomlin's editorial notes (1919 : 66), in which he stated that the de Burgh Collection was offered for sale and that it included *Thatcheria mirabilis*, frequently considered to be a monstrosity of *Fusus*. (Presumably Tomlin intended this to refer to the genus *Fusinus* Rafinesque 1815 emend. pro *Fusus* Lamarck 1799, *non* Helbling 1779).

Yokoyama (1928 : 338, pl. 66, figs. 3, 4) described and figured two specimens from the Pliocene of Japan as *Cochlioconus gradatus* gen. et sp. nov. The new genus was not explicitly referred to any family, but it was described as " *Conus*-like " and Yokoyama stated that " The presence of a deep sutural notch reminds us of the genus *Conus*." Pilsbry saw this paper and wrote to Yokoyama, drawing his attention to the similarity between *Cochlioconus* and *Thatcheria*. Yokoyama then stated in a subsequent paper (1930) that he regarded *Thatcheria* (*T. mirabilis*) and *Cochlioconus* (*C. gradatus*) as congeneric, though not conspecific, the Pliocene species being more *Conus*-like in appearance than the Recent form. He did not, however, change his views on the systematic position of the genus, for he wrote (p. 406) " I think I am right in placing it near *Conus*. This opinion seems to be also shared by Mr. Pilsbry as is evident from his communication." He also stated, probably wrongly, that Angas' specimen of *T. mirabilis* " may be the only one now existing [i.e., in a collection] in the whole world."

Thiele (1929 : 320) considered *Thatcheria* to be a synonym of the sub-genus (" sectio ") *Semifusus* sensu stricto, which he placed in the family Galeodidae. The proper family name is in fact Melongenidae, the name of the type-genus *Galeodes* being a junior homonym (Röding 1798 *non* Olivier 1791). Thiele, who was concerned only with Recent molluscs, did not mention *Cochlioconus*.

S. Hirase (1934 : 104, pl. 128B, fig. 3) figured a specimen of " *Thatcheria mirabilis* Angas (= *Semifusus m.*?) ", which is appreciably longer and more slender than Angas' type. The illustration is of interest in that it showed, for the first time, that more than one individual of the species had been found.

This point was emphasised in 1937 at an Ordinary Meeting of the Malacological Society of London, at which Tomlin exhibited two shells of the species, both from Japan. Hopwood wrote in the *Proceedings* (1937 : 158) that " Tryon's dictum [that *Thatcheria* is a scalariform monstrosity] has been confuted recently by the discovery of several examples, but where it should be placed systematically is as great a problem as ever. Discussion elicited suggestions that it was a prosobranch to be placed in Turridae and that it was an opisthobranch allied to *Akera*." The suggestion that it was a turrid had not been made before.

The first recorded find of the soft parts of *Thatcheria* was made at about this time ; Tomlin had obtained from a Japanese fisherman the anterior portion of a male animal, which was described and figured by Eales (1938). Unfortunately the specimen had lost the radula. Eales concluded, however (p. 16), that its characters " show that the specimen belongs to the Toxoglossa." A comparison of the creature with various members of the Turridae (e.g., *Turricula javana*) and of the Conidae (e.g., *Conus quercinus*) showed a very close resemblance to the former and none whatever to the latter ; and an X-ray photograph of the shell of *T. mirabilis*, which " shows a typical columella similar to that of the Turrids, not resorbed as in the Cones ", confirmed Eales' opinion (p. 17) that " As far as it is possible to judge . . . *Thatcheria mirabilis* should be placed with the Turrids."

The next paper to mention *Thatcheria* was that of Powell (1942), in which he suggested a close affinity between *Thatcheria* and the fossil *Waitara*. At this point it is necessary to digress a little upon the latter genus.

All the species mentioned immediately below and referred to *Waitara* are from New Zealand. Marwick (1926 : 324, pl. 74, fig. 9) had described a specimen from the Upper Miocene under the new specific name *waitaraensis*, referring it to the genus *Turricula* ; but he also wrote (p. 326) that " the generic location of the Turridae described above is quite provisional. New genera seem to be required ". Later

(1931 : 149) he erected the new genus *Waitara* upon this species, and referred thereto another new Miocene species, *W. generosa* (pl. 18, fig. 339). Powell (1942 : 168) considered *W. generosa* to be of Lower Miocene age. Powell also described two more species of *Waitara* in the same work—*W. pagodula* (p. 168, pl. 14, fig. 7) from the Upper Miocene or Lower Pliocene and *W. liratula* (p. 169, pl. 14, fig. 8) from the Lower Pliocene—and mentioned yet another Lower Pliocene species (p. 168), represented by a single specimen too poorly preserved for description or illustration but said to be " somewhat similar [to *W. pagodula*] but narrower ". The *Waitara liratula* material included the protoconch illustrated in his text-fig. B3 (p. 38). The paper gave a key to the four named species of *Waitara* (p. 168).

Powell's systematic conclusions were important. He wrote (p. 167) " It is possible that *Waitara* may yet prove to be identical with *Thatcheria* . . . and *Cochlioconus* . . . In any case all three are closely allied and represent a discordant Turrid-like group that cannot be satisfactorily placed in any of the nine sub-families adopted in this bulletin. . . . *Cochlioconus* is almost certainly a synonym [of *Thatcheria*], although its author made no reference to *Thatcheria*, but compared his genus with the Cones. Anyone acquainted with *Thatcheria* would scarcely have overlooked the need for some comparison." Evidently Powell did not know of Yokoyama's second paper on this subject ; nor, indeed, does he seem to have been aware of Eales' work. He sought to differentiate *Waitara* from *Thatcheria*, at least provisionally, because its sinus " although very similar to that of *Thatcheria*, does differ at its point of origin, in being narrowly concave before swinging forward, whereas the sinus in *Thatcheria* swings forward immediately." He also described the form of the sinus in all these genera as " deep Conid-like." Finally, after discussing the relationship of the genera in question to certain sub-families of the Turridae (the Daphnellinae and the Cochlespirinae) and to the Conidae, Powell came to the following conclusions (p. 168) :

" In order not to prejudice the status of the other Turrid subfamilies by forcing in such an aberrant group, it seems advisable to consider *Thatcheria* and its allies as representative of a new family, closely akin or parallel to the *Turridae*, for it seems to have arisen from the *Conidae*, but probably much later and independent of the early Conid-like Turrid divergent stock as represented by the *Conorbiinae*." He called this new family the Thatcheriidae ; and, in the same work (p. 170), he wrote " The former [i.e. the Thatcheriidae] in having marked Conid affinity in respect to its sinus is indicated as a late Tertiary offshoot from the *Conidae* . . . "

Wenz (1943) evidently saw no connexion between *Thatcheria*, *Cochlioconus* and *Waitara*, for he placed all three in different families. He considered *Thatcheria* (p. 1215) to be a synonym of the sub-genus *Hemifusus* of the genus *Pugilina* Schumacher 1817, family Galeodidae. *Cochlioconus* (mis-spelt " *Cochliconus* " in the text on p. 1470 and in the index on p. 1604, though correct in the legend to fig. 4154) he regarded as a sub-genus of *Conus* Linnaeus 1758, family Conidae. And he classified *Waitara* (p. 1390, fig. 3929) as a genus of the sub-family Clavatulinae, family Turridae ; he wrongly cited *W. generosa* Marwick as the type-species, wrongly quoted its horizon as *Upper* Miocene and gave the stratigraphical range of the genus as Oligocene to Miocene, although no Oligocene species of *Waitara* has ever been recorded. (The Pliocene species of *Waitara* described by Powell (1942) were, of course, unknown to Wenz because of the Second World War.) The genus *Clinura* Bellardi 1875 (see below) was also included by Wenz (p. 1390, fig. 3928) in the Clavatulinae, as a sub-genus of *Surculites* Conrad 1865.

Beets (1943*a* : 296) described as *Surculites* (*Clinura*) *bituminatus* a new species of gastropod from the asphalt deposits of the island of Buton, off Celebes ; the deposits were at that time believed to be of Upper Oligocene age. Like Wenz, Beets regarded *Clinura* as a sub-genus of *Surculites* and considered these forms to be turrids. In his description of *S.* (*C.*) *bituminatus* he placed *Cochlioconus* in the synonymy of *Clinura* ; but, when doing so, he knew nothing of *Thatcheria*, for it was not until later that Yokoyama's second paper (1930) drew his attention towards that genus.

Perhaps the most important work of all on this group of gastropods was a second article by Beets (1943*b*). He suggested that *Thatcheria* (including, *fide* Yokoyama, 1930, *Cochlioconus*), *Clinuropsis* Vincent 1913 (*non* Thiele " 1931 " [should be 1929]) and *Nekewis* Stewart " 1926 " [should be 1927] should all be regarded as junior synonyms of the sub-genus *Clinura*. In this paper Beets discussed a large number of species—of *Clinura*, of *Clinuropsis*, and of other genera such as *Cryptoconus*, *Surculites*, " *Pseudotoma* ", " *Surcula* ", " *Pleurotoma* " and "*Turricula* "—in order to ascertain whether they might properly be included in *Clinura* ; and, since he considered their great variations in form (especially that of the posterior sinus) to fall within the range of the "für die so schwierigen Turridae ' normalen Variabilität ' ", his decision was usually affirmative. He concluded (p. 365) : " *Clinura* ist jetzt mit Gewissheit bekannt aus dem Eocän bis Miocän der atlantischen [surely that should be " pazifischen "?] Küstenregionen Nordamerikas . . . , aus dem Montien bis Pliocän Europas und dem Oligocän des ostindischen Archipels ; in Japan tritt sie erst ins Pliocän auf und lebt dort mit einer einzigen, extremen rezenten Art fort. Vielleicht (?) ist *Clinura* auch noch bekannt aus dem Eocän S.W. Afrikas und des Congos, höchstens mit zwei Arten."

At this point it may be useful to give a short account of *Clinura* and of its author. The genus was erected by Aloysius Bellardi (1875 : 20) in a paper written entirely in Latin ; although " A. Bellardi " and " L. Bellardi " (Luigi) are sometimes listed separately in bibliographies (e.g., Wenz, 1944 : 1513), there are several reasons which make it seem certain that " Aloysius " was merely a latinisation of " Luigi " and not the name of another author. First, both " Aloysius " and Luigi were Professors of Natural History, living at the same time in the same country and writing on the same subject ; indeed, not only " Aloysius " but also Luigi published works concerned with *Clinura*, including the one mentioned below in which Luigi quoted verbatim (but without acknowledgment) the generic diagnosis given by " Aloysius " and then designated a type-species. Secondly, both " Aloysius " and Luigi published in the *Bullettino della Società Malacologica Italiana* ; and authors of works in that journal were generally members of the society in question, yet only Luigi's name is to be found in the list of members for 1875. Thirdly, " Aloysius " (unlike Luigi) published nothing except this one paper. Fourthly, neither " Aloysius " nor Luigi, when referring to names proposed by a Bellardi or to previous publications by a Bellardi, was in the habit of distinguishing himself from the other by the use of an initial. Fifthly, a paper in French by " Louis " Bellardi (1841) is clearly the work of Luigi ; it is therefore evident that Luigi was in the habit of altering his Christian name to conform with the style of the language in use. Finally, an obituary of Bellardi by his fellow malacologist Sacco (1889) gives a list of the " Publications scientifiques de M. Louis Bellardi " ; this includes all the works of " Aloysius ", Luigi and " Louis ", and thus provides conclusive proof of their identity.

The 1875 paper designated no type-species for *Clinura* but assigned two species to the new genus, *C. calliope* (Brocchi, 1814 : 436, pl. 9, figs. 15*a, b*) [*Murex*] and *C. elegantissima* (Foresti, 1868 : 598, pl. 2, figs. 10–13) [*Pleurotoma*] ; Bellardi placed *Clinura* in his new sub-family Pseudotominae, family Pleurotomidae. A far more complete account of the genus, published a few years later in Italian by Luigi Bellardi (1877 : 204–209), included five species therein ; *Clinura calliope,* from the Upper Miocene of Italy, was clearly designated as the type (p. 204). Other fossil species were subsequently referred to the genus, at first only from the Neogene of Europe, e.g., R. Hörnes & Auinger, 1891 : 362 ; Friedberg, 1912 : 210) ; later, however, species from rocks as old as the Eocene and as far away as California and Celebes were also placed in *Clinura* (e.g., Grant & Gale, 1931 : 494 ; Beets, 1943*a*, 1943*b*, as indicated above).

Meanwhile two Recent deep-sea gastropod species had also been referred to *Clinura, C. monochorda* Dall (1908 : 292, pl. 13, fig. 1) and *C. peruviana* Dall (1908 : 293, pl. 13, fig. 2). Since these are the only Recent species ever referred to the genus, they are also the only species mentioned by Thiele (1929 : 371), whose work did not deal with fossil forms. Thiele wrote of Dall's species, however, that " doch dürften sie mit dieser [*Clinura*] kaum verwandt sein ", without giving any reason for this statement, and he proposed that these two species should constitute a new section *Clinuropsis* of the genus *Pleurotomella* Verrill 1873, with *P.* (*C.*) *monochorda* (Dall 1908) as the type-species. But, by the time he wrote his " Nachträge und Berichtigungen " to the same work, published in 1934, Thiele had learnt that the name *Clinuropsis* had already been used by Vincent in 1913 ; he therefore proposed (p. 1002) the new name *Anticlinura* to replace it.

Wenz (1943 : 1460) treated the supposed Recent species of *Clinura* exactly as Thiele had done. Beets (1943*b* : 364) also agreed with Thiele (1929) in the matter, Dall's species being two of the few which he chose to exclude from the genus *Clinura* ; unlike Thiele, he gave reasons (such as the presence of lattice-like sculpture on Dall's species) for so doing. Further, Beets appears to have noted Vincent's preoccupation of the name *Clinuropsis* but not Thiele's subsequent correction and proposal of *Anticlinura* nom. nov. to replace *Clinuropsis* Thiele ; for he himself, with the same intention, proposed *Clinuromella* nom. nov. Thus *Clinuromella* Beets 1943*b* is an objective junior synonym of *Anticlinura* Thiele 1934, both being new names for *Clinuropsis* Thiele 1929 (*non* Vincent 1913). In conclusion, it would seem that Dall's two species should continue to be placed under the sub-generic name *Anticlinura* (of which *monochorda* is the type-species) in the genus *Pleurotomella.*

No author has ever disputed the position of *Clinura* in the Turridae (Pleurotomidae). Cossmann (1896) and Friedberg (1912) both regarded the taxon as a subgenus of *Surcula* H. & A. Adams 1853 ; but Grant & Gale (1931) considered it to be a sub-genus of *Surculites,* in which opinion, as recorded above, they were followed by Wenz (1943) and Beets (1943*a* ; 1943*b*). Wrigley (1939), however, while not denying the turrid (or at least toxoglossan) nature of *Clinura,* believed that *Surculites* was not a turrid and therefore not related to *Clinura.*

Thus the connexion of *Thatcheria* with *Clinura* was suggested and firmly established in 1943. The rest of this historical account will deal also with papers referring to *Clinura,* even though they make no mention of *Thatcheria.*

Though complete in most respects, Beets' paper (1943*b*) had not considered *Waitara.* Powell's bulletin on the Turridae, published in New Zealand in 1942, drew attention to the relationship between *Waitara* and *Thatcheria,* but had not been seen by Beets working in that same year in the German-occupied Netherlands ; nor could he have seen Wenz's treatise (1943) which placed *Waitara* immediately next to *Clinura.* In 1949, however, Beets obtained access to Powell's bulletin ; and in 1951 he published yet another paper, one part of which was concerned with " *Waitara* and its relationships to *Surculites-Clinura-Thatcheria.*" The main object of this work was to establish *Waitara* as part of " the species group *Clinura* . . . (taken in a broad sense) " ; the three taxa *Clinura, Waitara* and *Thatcheria,* hitherto related only as three different pairs by three different authors, were to be brought together. Beets recognised, however, that Wenz's conclusions regarding the taxonomic proximity of *Waitara* and *Clinura* had been based entirely on Marwick's original Miocene species of the former genus, while the affinities of that genus to *Thatcheria* depended more on the characters of the younger species described by Powell (1942).

One noteworthy point from Beets' 1951 paper is that, whereas he had earlier (1943*b*) considered *Thatcheria* to be a synonym of the sub-genus *Clinura,* he now regarded *Clinura, Waitara* and *Thatcheria* as three separate (but closely related) sub-genera, still in the genus *Surculites.* He gave no reason for this change. Incidentally, this work of Beets contains three minor errors. First, he stated (p. 14) that *Turricula waitaraensis* Marwick became the type-species of *Waitara* by Powell's subsequent designation in 1942 ; it was, in fact, the type-species by Marwick's original designation (1931). Secondly, he appeared to claim (p. 15) that he himself was the first to refer *Thatcheria* to the Turridae (1942*b,* cited in the present work as 1943*b*) ; he was, of course, preceded in this by Eales (1938). Thirdly, he quoted Powell (p. 16) as describing the posterior sinus of *Waitara* as " first narrowly convex " ; that should read " concave ".

Beets (1951) also gives a small, semi–schematical figure (pl. 1, fig. 6) of " *Thatcheria* spec. nov. ; a portion of a specimen from the Pliocene of East-Borneo ". The fragment was mentioned only briefly in the text (p. 16) and has not yet been described. It appears to consist of two whorls from a pagodiform spire which must indeed have been remarkably like that of *T. mirabilis,* with a similar type of sinuosity in the growth-lines on the ramp.

The asphalt deposits of Buton (which, according to Beets (1943*a* ; 1943*b*), contained two species of *Clinura*) were supposed to be of Upper Oligocene age. In 1953, however, Beets showed (p. 239) that the age of the molluscan fauna was most likely Mio-Pliocene ; there is no evidence to support the suggestion that the molluscs might be a mixture derived from different stratigraphical horizons, but the possibility cannot be entirely excluded. He also reported Reinhold as concluding that the diatoms in the deposits indicate a probable Upper Miocene age.

S. Hirase's posthumous handbook of Japanese shells (1951), which was in effect his catalogue of 1934 revised and enlarged by Taki, reproduced the figure of *Thatcheria mirabilis* which had appeared in the earlier work (pl. 128B, fig. 3, in both). The later work, however, no longer suggests that *Thatcheria* might be a synonym of " *Semifusus* " ; and the second edition (1954) is provided with a systematic index to the plates which, on p. 88, classifies *Thatcheria* as a genus of the Turridae.

Thatcheria was also listed among the Turridae by Kuroda & Habe (1952 : 10). On p. 90 of the same work they indicated that the geographical range of *T. mirabilis* was off the Pacific coast of Japan, between 33° and 35° of latitude.

Hatai & Nisiyama (1952 : 191) listed Yokoyama's two syntypes of *Cochlioconus gradatus* with full details of locality and horizon ; the latter was given as Takajo Formation, believed to be of Lower Pliocene age. It was noted that both specimens were in the collections of the Geological Institute of the Faculty of Science of Tokyo University. The specimen illustrated in Yokoyama's fig. 3 (1928, pl. 66) was designated as lectotype (" holotype ") by these authors, who evidently regarded *C. gradatus* as a junior synonym of *Thatcheria mirabilis.*

Kuroda & Habe (1954 : 80) published important new information on *Thatcheria mirabilis* ; this was obtained from three individuals of different ages, each with soft parts. They were able to describe and figure the radula (text-fig. 2) and the protoconch (text-fig. 1, showing also the early nepionic whorls) ; the operculum was reported lost in all the specimens. The peculiar shape of the radula and the obliquely reticulated sculpture of the protoconch led them to suggest that *Thatcheria* was a member of, or had a close affinity with, the Daphnellinae. Unfortunately they had misinterpreted both Eales' and Powell's papers. First, they thought that Eales' observation, " No traces of proboscis or radula are present ", indicated the natural lack of a radula in the species ; but, in fact, the lack of a radula was clearly accidental in the specimen which constituted the whole of Eales' material, " the body being torn away immediately posterior to the mouth tube." Secondly, they believed that Powell had established the family Thatcheriidae to include, not only *Thatcheria mirabilis* and some fossil species, but also some other, related Recent groups (but no others are known) ; and further, that Powell had done this because of the " nature of its radula quite rudimentary " in *Thatcheria* (also unknown at that time).

Habe (1955) devoted two short articles to " *Thatcheria mirabilis* Angas (Turridae) ". The first is in English ; it consists only of a direct quotation of Angas' description, reproductions of the figures of the early whorls and the radula (from Kuroda & Habe 1954), references to the works of Angas, Eales, Powell, and Kuroda & Habe, and the comment " This strange species seems better to locate under the subfamily Daphnellinae in having the reticulated protoconch and the dart shaped radula." The other article is in Japanese but is not the same ; it reproduces the illustrations to Angas' paper, cites the dimensions of three new specimens of *T. mirabilis* and mentions the fossil *Cochlioconus*.

Kira (1955 : 71, pl. 35, fig. 19) also placed *Thatcheria mirabilis* in the Turridae.

Rossi Ronchetti (1951–56) included *Murex calliope*, the type-species of *Clinura* (see p. 263), among the species dealt with in her review of Brocchi's types; she selected, figured and carefully described a neotype (1955 : 305, fig. 163) because Brocchi's holotype was no longer preserved. The species appears, however, under the name *Pleurotomella* (*Clinuropsis*) *calliope*, presumably for the following reasons:

The introduction to Rossi Ronchetti's review stated (1951 : 11) that the revision of the generic names would be based partly upon the works of Wenz (1938–44) and Schilder (1932), partly upon the works of Thiele (1929–31, 1934–35). Schilder, of course, dealt only with Cypraeacea. In this particular instance Rossi Ronchetti could not have used Wenz (or Thiele's "Nachträge und Berichtigungen") as the basis for her classification; had she done so, she would then have known—as she clearly did not know—that Thiele had later proposed *Anticlinura* as a new name to replace his own *Clinuropsis*. It therefore appears likely that she based her classification only upon Thiele's main work. Noting that Dall's species of *Clinura*, the only supposed representatives of that genus mentioned by Thiele, had been transferred by the latter author to *Pleurotomella* (sectio *Clinuropsis*), Rossi Ronchetti did the same with *Clinura calliope*—probably without considering the possibility that Dall's species had no real connexion with *Clinura*.

Although other authors may not agree that *calliope* Brocchi and *monochorda* Dall are co-sub-generic, or even congeneric, Rossi Ronchetti is nevertheless entitled to her opinion that they are. In that case she was correct in using for both species the oldest generic name available—*Pleurotomella* Verrill 1873. But, for the sub-genus, she should then have used the oldest generic name previously applied to any included species—and this was *Clinura* Bellardi 1875, not *Clinuropsis* Thiele 1929 (which, in any case, was preoccupied). Moreover, according to Grant & Gale (1931 : 510), *Pleurotomella* Verrill 1873 (type-species *P. packardii* Verrill 1873) is a subjective junior synonym of *Pleurotomoides* Bronn 1831 (type-species *Defrancia pagoda* Millet 1826).

With respect to *Clinura*, Eames (1957 : 51) adopted the classification of Grant & Gale, Wenz, and Beets, in which *Clinura* appears as a sub-genus of *Surculites* in the Turridae. But he referred the Eocene species *Surcula ingens* (Mayer-Eymar 1896) [*Pleurotoma*] to *Clinura*, although Beets (1943*b* : 363) had clearly expressed the opinion that it was not related thereto and represented an altogether different group.

The Fiji Geological Survey Department, in its Annual Report for the year 1958 (1959), mentioned on p. 15 the collection of an unusual fossil shell from the island of Vanua Levu, identified by the present writer as a new species of *Thatcheria*. The Report also quoted his observation (in litt.) " . . . as far as I am aware, the genus has never been recorded as a fossil."

Several gastropod species represented in the collections of the Institut Royal des Sciences Naturelles de Belgique were listed by Glibert (1960 : 25) under the generic name *Clinura*. They are all from the Tortonian or Plaisancian of Italy or the Vienna Basin. Glibert classified *Clinura* as a genus of the sub-family Cochlespirinae (family Turridae).

TABLE I.—SUMMARY OF VIEWS ON SYSTEMATIC POSITION OF *THATCHERIA*

(i.e., of the only two named species hitherto referred to that genus)

Author	Sp.	Sub-genus	Genus	Sub-family	Family
Sowerby, 1880	*m*		*Pyrula* (juvenile) (= *Ficus*)		[Pyrulidae (= Ficidae)]
Tryon, 1881, 1883	*m*		*Thatcheria*, a scalariform monstrosity listed under *Hemifusus*	Melongeninae, Melongeniinae	Buccinidae
Pilsbry, 1895	*m*		*Thatcheria*		
Thiele, 1929	*m*	*Semifusus* s.s. (= *Hemifusus* s.s.)	*Semifusus* (= *Hemifusus*)		Galeodidae (= Melongen dae)
Wenz, 1943	*m*	*Hemifusus*	*Pugilina*		
Pchelintsev & Korobkov, 1960	*m*		*Hemifusus*		
Fischer, 1884 Cossmann, 1901	*m*		A scalariform monstrosity of *Semifusus* (=*Hemifusus*)	Melongeninae	Turbinellidae
Cossmann, 1889	*m*		*Mayeria*		
Angas, 1877	*m*		*Thatcheria*	Fusinae (= Fusininae)	[Fusidae (= Fusinidae
Tomlin, 1919	*m*		A monstrosity of *Fusus* (= *Fusinus*)	[Fusinae (= Fusininae)]	
Hopwood, 1937	*m*		*Thatcheria*		? Turridae
Eales, 1938 Kuroda & Habe, 1952 Hirase & Taki, 1954 Kira, 1955	*m*		*Thatcheria*		Turridae
Beets, 1943*a*	*g*	*Clinura*	*Surculites*		
Beets, 1943*b*	*m g*	*Clinura*	*Surculites*		
Beets, 1951	*m g*	*Thatcheria*	*Surculites*		
Kuroda & Habe, 1954	*m*		*Thatcheria*	Daphnellinae	[Turridae]
Habe, 1955	*m g*		*Thatcheria*	Daphnellinae	Turridae
Powell, 1942 MacNeil, 1960	*m g*		*Thatcheria*		Thatcheriidae
Yokoyama, 1928	*g*		*Cochlioconus*		[Conidae]
Yokoyama, 1930	*m g*		*Thatcheria*		
Wenz, 1943 Pchelintsev & Korobkov, 1960	*g*	*Cochliconus* (= *Cochlioconus*)	*Conus*		Conidae
Hopwood, 1937	*m*		*Thatcheria*		? [Akeridae]
Charig, 1963	*m g*		*Thatcheria*	Thatcheriinae	Turridae

Note :

m indicates application to *mirabilis* Angas.

g indicates application to *gradata* Yokoyama.

Square brackets [ ] denote implicit references.

Where an author has used a junior synonym or homonym, or family name derived therefrom, the nan considered here to be correct is also given—in parentheses.

The *Osnovy Paleontologii* (1960), edited by Pchelintsev & Korobkov, adopts a very conservative arrangement which seems to be based on that of Wenz; the important works of Eales, Powell, Beets, and Kuroda & Habe are all ignored. *Thatcheria* (p. 222) is given as a synonym of the genus *Hemifusus*, family Galeodidae; *Cochlioconus* (p. 241), again mis-spelt "*Cochliconus*", appears as a sub-genus of *Conus*, family Conidae; *Waitara* (p. 240) is cited as a genus *incertae sedis* in the Pleurotomidae; and, in that same family, *Clinura* (p. 239) is still considered to be a sub-genus of *Surcula*.

MacNeil (1960 : 120, pl. 15, figs. 11, 12) described two shells from the Neogene of Okinawa, now in the United States National Museum, as *Thatcheria* cf. *T. gradata* (Yokoyama); he retained Powell's family Thatcheriidae for the genus. The figured specimen was from the Pliocene; the other was from rocks which might be a little older, perhaps of either [Lower] Pliocene or [Upper] Miocene age. Both were compared with *T. gradata* rather than with *T. mirabilis* because of their plane to slightly concave ramp (the ramp in *T. mirabilis* is "definitely depressed with the periphery slightly upturned"), the coarser sculpture, the lack of crowded spirals just below the periphery, and (presumably) the less pagodiform spire. The excellent preservation of the Okinawan specimen figured by MacNeil, with the sculpture preserved nearly to the protoconch stage, shows that "The early sculpture is strongly turrid, the periphery being ornamented with well defined blunt denticulations, about 9 or 10 visible from an angle, and the denticulations themselves are crossed by fine spiral lines"; in this respect comparison with Yokoyama's material is impossible, for the early whorls are not preserved in either of the Japanese specimens. Nor, for that matter, are they preserved in MacNeil's other Okinawan (possibly Miocene) specimen.

MacNeil also expressed some slight doubt as to whether the young shell figured by Kuroda [& Habe] (1954) was really a *Thatcheria*, pointing out that the first nepionic whorl is quite different from that of the Okinawan form. The figured specimen from Okinawa, however, lacks more of the apex than is represented by the whole of Kuroda & Habe's figure, and therefore a proper comparison cannot be made.

III. NOTES ON *THATCHERIA MIRABILIS* ANGAS

Identification of the holotype

It was suspected that the holotype of the species might be a shell in the collection of the Department of Zoology of the British Museum (Natural History), recently registered under the number 1960.154. The only available information pertaining to this specimen is that it formed part of the de Burgh Collection.

As mentioned above (p. 258), Angas gave no indication as to where his unique shell was deposited. But Sowerby wrote that it was "in the collection of Mrs. Deburch"; and a copy of Angas' original paper, now in the possession of Mr. S. P. Dance, bears the annotation "de Burgh Coll." in Fulton's handwriting. Finally, as also mentioned above, the de Burgh Collection was offered for sale in 1919 and included material of *T. mirabilis*. Although it was not stated explicitly that there was only one specimen, there is nothing to suggest that there was more than one; indeed, it was not until the nineteen-thirties that it became apparent that *T. mirabilis* was not just a unique monstrosity.

The British Museum specimen referred to has therefore been compared with Angas' description and illustrations. Its dimensions and individual peculiarities, especially the form of the mended break in the outer lip, show that, while the drawings (which bear the indication " G. Sowerby lith.") are not wholly accurate, the common peculiarities are so many that they cannot be merely fortuitous.

It may therefore be presumed that the B.M. specimen, registered number 1960. 154, is the holotype of *Thatcheria mirabilis* Angas.

Additional material in the British Museum

(1) The incomplete soft parts described by Eales (1938) (B.M. regd. no. 1937–12–16.1). This specimen was obtained at Kii, Japan, and was presented to the Museum by Tomlin in 1937. The shell is missing, but it must be presumed that one was originally associated with these soft parts, for the latter could not otherwise have been identified ; it may have been one of the two exhibited by Tomlin in 1937 at a meeting of the Malacological Society of London. (Tomlin's collection, lodged in the National Museum of Wales, Cardiff, includes two uncatalogued shells of *Thatcheria mirabilis* from Kii, and it seems likely that these are the same two.) Dr. Eales has no information on the subject.

(2) The shell of which an X-ray photograph was given in Eales' (1938) paper. This photograph was of " a specimen in Mr. Winckworth's collection ". Winckworth's entire collection was later bought by the British Museum ; the shell shown in the photograph may therefore be in the Museum's possession, but it cannot be found at present.

(3) Another shell (B.M. regd. no. 1937–7–9.40). This specimen is considerably smaller than the holotype (length 76 mm. as against 87 mm.). It too was obtained at Kii, Japan, and was bought from H. C. Fulton in 1937. It is certainly not the X-rayed specimen.

Supplementary description

Angas (1877) described *Thatcheria mirabilis* as having an " outer lip with a broad excavated sinus extending from its juncture with the body-whorl to the extremity of the last keel " ; he gave no more precise indication of its form. His fig. 1*a* of the shell in apical view shows the margin of the posterior sinus (and all the collabral growth-lines parallel thereto) intersecting the edge of the preceding whorl more or less at right angles ; as the margin passes outwards from that point it at once curves smoothly forward and then runs obliquely to meet the carina at an acute angle. His fig. 1*b* of the same shell in apertural view gives no more information on this matter.

It is nevertheless obvious that, since each whorl is much wider at the carina than at the abapical suture, it will hide the inner part of the ramp of the following whorl when viewed from the direction of the apex ; thus, in Angas' figure, the line which seems to terminate the margin of the sinus at its inner end is the carina of the preceding whorl. The margin of the sinus must in fact pass further adaxially beneath the carina to meet the (hidden) adapical suture. But what is the precise form of this inner part of the sinus margin?

Except for one drawing by Beets (1943*b*, referred to below), the work of subsequent authors has done nothing to make known the form of the posterior sinus in *Thatcheria mirabilis* ; sometimes, indeed, the form of the sinus has been completely misunderstood. The holotype will therefore be briefly re-described, with particular reference to that feature.

The form of the sinus is clearly shown in Plate 47, fig. 3. The margin of the sinus does not pass perpendicularly outwards from its point of origin on the adapical suture, but extends obliquely outwards and backwards for a short distance ; as it does so it curves right round until it is running obliquely forwards to meet the carina at an acute angle. The outer limb of this arch is much longer than the inner, so that any given growth-line meets the carina at a point which is much further forward than its point of origin, and the vertex or base of the sinus lies much nearer to the suture than to the carina—at about a quarter of the distance across the ramp. This type of sinus may be described as deep and juxtasutural, its depth being largely due to the forward extension of the outer lip.

Powell (1942 : 167) was entirely misled by Angas' figure. He wrote that " *Thatcheria* has . . . a very deep sutural sinus " ; but, as mentioned above, he noted that *Thatcheria* seemed to differ from *Waitara* in that its sinus swung forward immediately from its point of origin.

Beets, on the other hand, seemed to understand the true nature of this sinus. In his drawing of *T. mirabilis* in apical view (1943*b*, pl. 36, fig. 2) the position of the suture, hidden by the projecting carina of the preceding whorl, is marked with a broken line ; also marked are the whole of the margin of the sinus and of one growth-line, rightly showing the hidden parts next to the suture passing backwards in an arc. However, he paradoxically wrote (p. 361) : " Der Sinus der Aussenlippe ist vollkommen vergleichbar jenem der (anderen) *Clinura*-Arten ". Now this is true. But, as shown below, his conception of the form of the posterior sinus in *Clinura* was itself completely wrong ; it was based on the misleading illustrations of other authors, so that he believed the sinus to be quite shallow. Further, he cited (Beets, 1951 : 16) Powell's observations on the *Thatcheria* sinus, yet at the same time was puzzled by the apparent fact that the sinuses of *Cochlioconus* and *Waitara*, while similar to each other, differed from that of *Thatcheria* in that they were first narrowly concave.

The superficial ornament of the shell is another feature of *T. mirabilis* that has not been adequately described. Angas (1877) wrote of his holotype : " above the keels finely arcuately striate [i.e. with collabral growth-lines parallel to the margin of the posterior sinus], below irregularly more or less crenately concentrically ridged ". Beets (1943*b* : 361) included this description of the superficial ornament of *T.*

mirabilis : " der Kiel ist glatt, auch der obere Windungsabschnitt ; vor der Kante sind die Umgänge wieder fein spiralig gefurcht."

There are, in fact, three distinct categories of superficial ornament. These are spiral ornament, running in the direction of growth of the helicocone ; transverse ornament, running across (more or less) the direction of growth of the helicocone ; and collabral ornament (growth-lines), parallel to the outer lip throughout the length of the latter. Transverse ornament, of course, is usually collabral, but is not necessarily so (Cox, 1955 : 198).

In *Thatcheria mirabilis* there are indeed many distinct spiral furrows on the outer face, often arranged in pairs (Pl. 47, fig. 1). On the lower part of the outer face of the last whorl, within the inner lip, the furrows are soon obliterated by the forward growth of the edge of the mantle ; thus each spiral furrow, if traced backwards and inwards for a few millimetres beyond the inner lip, disappears beneath a shining white layer of callus. The carina of the shell is smooth. Very weak spiral striations are present on the ramp, except on its innermost part next to the adapical suture.

Transverse ornament is entirely lacking in *T. mirabilis.*

As for collabral lines, the form of the outer lip which produces them is simple and slightly convex between the anterior canal and the carina. On the ramp the outer lip delimits the posterior sinus, of which the form has already been described.

A final point to mention is that consideration of the length of all the nine measured shells of *T. mirabilis* recorded in the literature and in this present work leads to the conclusion that the holotype is an adult shell of average size. The measured lengths are 18 mm., 33 mm., 76 mm., 77 mm., 87 mm. (holotype), 89 mm., 94 mm., 97 mm. and 98·5 mm. Three other shells have been mentioned but without measurements ; they are the third specimen of Kuroda & Habe (1954), which is presumed not to be the same as any of the three referred to by Habe (1955), and Tomlin's two shells in the National Museum of Wales. Thus, in all, twelve shells have been mentioned hitherto. There is at least one more shell in a private collection in England, there are probably several in the United States, and it is likely that there are further specimens in Japan and elsewhere. Indeed, *Thatcheria mirabilis,* once thought to be a unique monstrosity, is no longer even a great rarity.

IV. NOTES ON *CLINURA*

Material studied

The British Museum collections contain two well preserved specimens of *Clinura* ; one of these belongs to the type-species *C. calliope.* The determinations were verified by detailed comparisons with the descriptions and figures of the original authors. Particulars of the specimens are as follows :

(1) *Clinura calliope* (Brocchi 1814) [*Murex*]. Brit. Mus. (Nat. Hist.) regd. no. G. 79439.

From the Plaisancian (Lower Pliocene) of Biot, near Antibes, Alpes Maritimes, France.

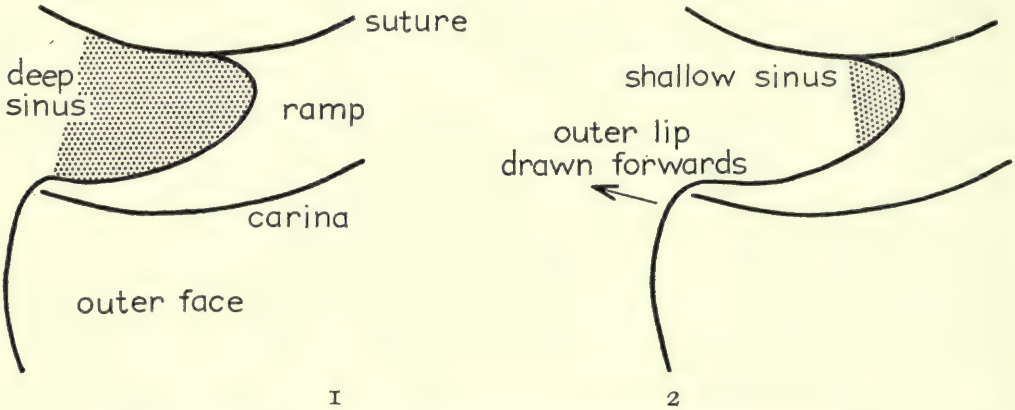
(2) *Clinura trochlearis* (M. Hörnes 1854) [*Pleurotoma*]. Brit. Mus. (Nat. Hist.) regd. no. GG. 2185. (This specimen was formerly in the Wrigley Collection.)

From the Zweite Mediterran-Stufe (Middle or Upper Miocene) of Walbersdorf, Burgenland, Austria.

This material was studied in order to ascertain the generic characters of *Clinura* rather than the specific characters of *C. calliope* or *C. trochlearis*. Since the former is the type-species, the latter was considered only in so far as it afforded additional evidence of those generic characters.

Posterior sinus

It is evident from Plate 47 that the posterior sinus of *Clinura calliope* (fig. 11) was exactly like that of *Thatcheria mirabilis* (fig. 3). But, just as in *T. mirabilis*, the form of the posterior sinus is not so readily apparent from the descriptions and has often been misunderstood—though in an entirely different way. In these fossil gastropods the outer lip with its sinus is usually broken away, and the form of the sinus must therefore be inferred from the form of the collabral growth-lines. Some of the earlier figures (and hence later ones copied from them) either did not show the growth-lines or else depicted them inaccurately ; and it is unfortunate that later workers have sometimes ignored descriptions in foreign languages. Finally, the posterior sinus of *Clinura* has been variously described as " deep " or " shallow ", even by the same author ; this point requires explanation.



FIGS. 1 and 2.—Alternative ways of describing the posterior sinus of *Clinura* and *Thatcheria*.

Confusion has probably arisen over the depth of the posterior sinus for the following reason. Some workers (including the present writer) define the posterior sinus as including the whole of the notch between the outer lip and the suture (Text-fig. 1). Others, however, have considered it to end anteriorly (with respect to the direction of growth of the helicocone) at the level of the junction of its margin with the suture (Text-fig. 2) ; in which case the sinus of *Clinura* must be regarded as shallow, but it is then necessary to mention that there is also a well developed forward extension of the outer lip.

The original author (Brocchi, 1814, pl. 9) gave two figures of *Murex calliope* which were repeated in the later edition of his work (1843). His fig. 15*a*, in apertural view, shows nothing of the growth-lines on the ramp ; but fig. 15*b*, in abapertural view, shows them fairly well. All that Brocchi wrote in this connexion (p. 436) was " . . . si osservano alcune finissime rugosità oblique ed arcuate che sono le tracce dell'antico margine di quella sinuosità, che hanno tutte le pleurotome nel labbro destro, e ch'è il carattere del genere."

Bellardi (1847, pl. 1, fig. 9) depicted *Pleurotoma calliope* with strongly curved growth-lines in which both limbs of the arch appeared to be of about the same length ; that is, the sinus would have been deep but symmetrical.

The same author (1875 : 20), proposing the new genus *Clinura*, gave only a generic diagnosis in Latin. This included two phrases which he later reproduced more grammatically (Bellardi, 1877 : 204) as " Sinus posticus labri sinistri valde profundus, arcuatus ; labrum sinistrum antice valde productum, aliforme ". But he also wrote on p. 204 : " I caratteri principali di questo genere sono [inter alia] :

3° labbro sinistro sinuoso posteriormente ;

4° seno molto largo e poco profondo, foggiato ad arco, il quale parte direttamente dalla sutura posteriore ;

5° labbro sinistro protratto a guisa di ala ".

It is not easy to reconcile " sinus . . . valde profundus " with " seno . . . poco profondo "! Incidentally, it should be noted that the outer lip is the " labbro destro " of Brocchi but the " labbro sinistro " of Bellardi. In Bellardi's figure (1877, pl. 7, fig. 1) the little that can be seen of the growth-lines makes the sinus appear shallow.

Cossmann (1896 : 74) described the sinus of *Clinura* as " largement arrondi en quart de cercle incomplètement fermé et aboutissant presque perpendiculairement à la suture ". His pl. 5, fig. 19 shows nothing whatever of the growth-lines.

It is evident that Grant & Gale (1931 : 494) based their idea of the form of the sinus in *Clinura* upon these works of Bellardi (1877) and Cossmann (1896), for they referred specifically to the figures of *C. calliope* therein. Thus they were led to write of the genus " posterior notch very wide and shallow, rounded ". They also transferred to *Clinura* certain American species which, in fact, differ widely from *Clinura* in the form of their sinus.

Of modern authors, only Wrigley (1939 : 283) seems to have been aware of the true form of the posterior sinus in *Clinura* ; for he wrote of that genus, " the growth lines sweep back over the rear slope four or five times as far as those of *Surculites* ". This character was not illustrated in his paper. Wrigley was wrong, however, in stating that *Nekewis io* (Gabb), from the Eocene of California, was much like *Clinura* ; for Stewart's figure of that species (1927, pl. 30, fig. 11) shows a fairly shallow, symmetrical sinus.

Beets (1943*b* : 359) cited the figures of Brocchi, Bellardi and Cossmann mentioned above, and then wrote : " Wie die Aussenlippe vor der Kante verläuft, ist nicht aus Bellardi's Abbildung abzulesen, wohl aber aus den anderen zitierten Figuren." His semi-diagrammatical drawing (1943*b*, pl. 36, fig. 8, pl. 37, fig. 23 ; 1951, pl. 1, fig. 3) is nevertheless based upon Bellardi's figure, to which has been added a growth-line evidently consequent upon a very shallow sinus. Thus Beets too had been misled.

Rossi Ronchetti (1955 : 306) was not informative on this point. She wrote of "*Pleurotomella*" *calliope* that "la maggior parte della superficie [della porzione posteriore . . . è] percorsa solo da strie di accrescimento alquanto arcuate." Her fig. 163 shows but the faintest trace of growth-lines, and then only the part nearest to the adapical suture.

As for *Clinura trochlearis*, examination of the material in the British Museum shows that its posterior sinus is just like that of *C. calliope*. Indeed, the form of the sinus in *C. trochlearis* was depicted very clearly by M. Hörnes in the figures to his original description (1854 : 363, pl. 39, figs. 14*a*, *b*, 15*a*, *b*) [*Pleurotoma*]; it has never been subject to misunderstanding.

Protoconch

No protoconch has yet been described in any species of *Clinura*; it may be that the apex of the shell was missing in all the material available to those working on the genus. But the two specimens in the British Museum, of which details have been given above, both possess a protoconch.

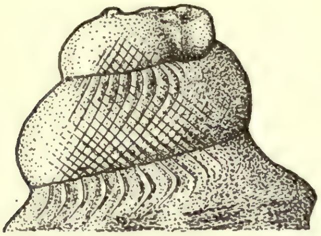
The protoconch of *C. calliope* (Pl. 47, fig. 12; Text-fig. 3) is well preserved, though probably incomplete above; two whorls remain. It is entirely covered with very distinct oblique cancellation, each thread being slightly concave towards the anterior side.

The protoconch of *C. trochlearis* (Text-fig. 4), of which two and a half whorls are preserved, is rather abraded. The upper and lower parts of each whorl are obliquely cancellate, just like the protoconch of the type-species, but the central, thickest part is worn smooth in places.

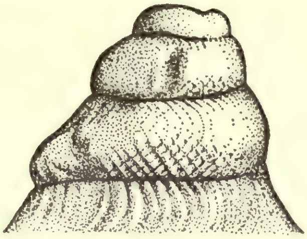
Transverse sculpture

The presence of transverse sculpture is well known in *Clinura calliope*. It consists of prominent tubercles on the carina; according to Rossi Ronchetti there are eighteen per whorl, but in fact the number increases with the size of the helicocone from not more than ten to at least twenty. Further, on the early whorls of the teleoconch each tubercle is continued abapically as a short, broad, slightly opisthocline rib running down the outer face (see Pl. 47, fig. 12).

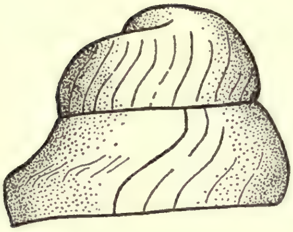
There is no record of any comparable sculpture in *C. trochlearis*; indeed, Hörnes (1854 : 364) described his new species as having "nicht eine Spur von Spitzen oder Dornen an dem Kiele, selbst an den obersten Windungen". This is certainly true of all the larger whorls. But the British Museum specimen shows that, just as in *C. calliope*, the first two and a half whorls of the teleoconch bear small nodules on the carina, about twelve on the first whorl and sixteen on the next; each has a small rib beneath it. As the helicocone grows these successively diminish in relative size and eventually disappear.



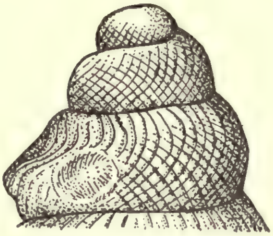
3



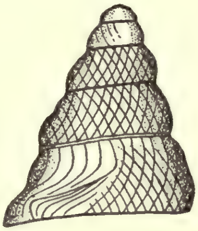
4



5



6



7

FIGS. 3–7.—Protoconchs :

3. *Clinura calliope* (Brocchi) ; original drawing by D. L. F. Sealy, based on a photograph of specimen no. G. 79439 in the British Museum (Natural History).
4. *Clinura trochlearis* (M. Hörnes) ; original drawing by D. L. F. Sealy, based on a photograph of specimen no. GG. 2185 in the British Museum (Natural History).
5. *Waitara liratula* Powell ; after Powell.
6. *Thatcheria mirabilis* Angas ; after Kuroda & Habe.
7. *Cryptodaphne pseudodrillia* Powell ; after Powell.

V. NOTES ON *WAITARA LIRATULA* POWELL

Protoconch

Powell (1942) was the first to postulate a close affinity between *Waitara* and *Thatcheria*. He mentioned that comparative studies of the protoconchs had yet to be made ; for, in any of the genera with which this work is concerned, the only protoconch known at the time was that of *W. liratula* described by Powell himself. Since then the protoconch of *Thatcheria mirabilis* has been described and figured by Kuroda & Habe (1954) from a beautiful specimen showing very distinct oblique reticulate ornament, and the remarkably similar protoconchs of two species of *Clinura* have now been described in the preceding section of the present work. If *Clinura*, *Waitara* and *Thatcheria* are indeed closely akin, it would be expected that the protoconchs also would be alike ; this expectation is rendered even more probable by the *Clinura*-like tuberculation of the carina on the first few whorls of the *W. liratula* teleoconch, noted below. But, according to Powell (1942 : 169), *W. liratula* has a " dome-shaped protoconch of two whorls bearing weak protractively arcuate axial growth threads " ; and his drawing (text-fig. B3 on p. 38 ; Text-fig. 5 in the present work) shows no ornament other than faint, slightly sinuate, slightly opisthocline striations, with no indication of others running across them. Might not this appearance have been caused by abrasion?

It was felt that the protoconch of *Waitara liratula* should be looked at again. According to Fleming (in litt.), " The paratype figured by Powell (pl. 14, fig. 8) is apparently the same specimen on which he based his text-fig. B3 . . . The holotype and other paratypes are still more deficient in protoconch. . . . We have no evidence whether the protoconch was damaged after Powell's figure was made." The figured paratype (Pl. 47, fig. 7) was therefore sent to London and examined with great care. Unfortunately the specimen does seem to have been damaged since Powell described it twenty years ago, for, whatever its condition before, the protoconch is now in such a poor state of preservation that it is difficult to compare it with Powell's drawing and impossible to see any traces of its original ornament. Indeed, the protoconch is far too worn and damaged to afford positive evidence of any significant difference between *Waitara* and *Thatcheria* in this taxonomically important character. A close relationship between *Waitara* and *Thatcheria*, as originally suggested by Powell himself, is therefore still quite possible.

Transverse sculpture

During the examination of the figured paratype of *Waitara liratula* it was noticed that the first two or three whorls of the teleoconch bore unmistakable indications of nodules on the carina, arranged with an appearance of regularity. The angular distance between consecutive nodules was estimated at about 20° of arc; thus, originally, there would have been about eighteen nodules per whorl. Beneath some of these there were traces of a short, broad and markedly opisthocline rib running down the outer face of the whorl. After the first few whorls, however, the carina became smooth. This character has not previously been recorded in *W. liratula*.

The Neogene shells from Okinawa which MacNeil (1960; see above, p. 268) described as *Thatcheria* cf. *gradata* seem to have a close affinity with *W. liratula*, even though it must be admitted that comparisons are difficult when they have to be made from one illustration of a single incomplete specimen of each species. The early whorls of the teleoconch of the figured specimen from Okinawa are far better preserved than in Powell's specimen and bear distinct nodules on the carina, exactly like those of *Clinura calliope*; these gradually become less distinct and eventually disappear at a point where the transverse diameter of the shell (measured across the carina) is about 4 mm.

Marwick (1931 : 149) reported that the early whorls of *W. generosa* bore about twelve low, rounded axial costae extending downwards from the keel and forming weak tubercles at their intersection with the shoulder-angle.

VI. SYSTEMATICS

General principles

The classification of the gastropods discussed in this work, except that of the Recent *Thatcheria mirabilis*, is necessarily based entirely upon their shell characters.

It has been generally believed that the most fundamental of these are the position and form of the posterior sinus, indicated in incomplete specimens by the position and form of the collabral growth-lines; this feature is considered to be the most useful of those by which a turrid may be distinguished from other Toxoglossa and assigned to a sub-family within the Turridae. But the posterior sinus is not infallibly diagnostic in these matters. In the Conidae, which are without doubt close relatives of the Turridae, the form of the posterior sinus varies not only from species to species but even within a species, and it is sometimes just like that of certain Turridae. For example, the collections of the British Museum (Natural History) include a series of shells of the Recent *Conus pennaceus* Born 1780, all characterised by a particular colour pattern. One of these, however, has a posterior sinus which resembles that figured by Powell (1942, text-fig. F28) as belonging to the Recent turrid *Asperdaphne versivestita* (Hedley 1912) [*Daphnella*]; another has the " reversed L " sinus more typical of the Daphnellinae (as found in *Daphnella cancellata* Hutton 1878); in a third specimen the sinus is similar to that of *Clinura* or *Thatcheria*; and in a fourth it is virtually absent. In other individuals it is yet again quite different from any of these. Thus there can be no such thing as a sinus typical of the Conidae, although Powell (1942 : 167), who mentioned the " deep Conid-like " sinus of his Thatcheriidae, clearly implied that there was. Again, Powell (p. 28) wrote of the Turridae that " Position and style of sinus is the best guide to subfamily grouping." Experience may indeed have shown that there is no better, but the guidance afforded by the posterior sinus provides no simple key to this problem; its form, if not its position, may vary widely within a given subfamily. In short, the posterior sinus appears to be of systematic value only when the taxonomic placing indicated thereby is confirmed by other distinctive characters with which it has no connexion.

It was therefore necessary to bear other characters in mind when considering whether or not the molluscs in question should be referred to the Turridae and, if so, to which particular sub-family thereof. Those characters were the nature of the protoconch and the absence of a tendency towards the resorption of the columella and early internal walls. Further, when a series of shells was thus referred to a given grouping, their possession of a common suite of less distinctive characters (such as a pagodiform spire, a certain distribution of spiral ornament, and a certain type of columella) offered additional confirmation of their relationship.

Generic and specific separation were effected primarily upon the presence or absence of transverse sculpture and tubercles, and secondarily upon a number of other characters—the position of the carina on the whorl, the degree of development and precise nature of the spiral ornament, the degree of " pagodiformity ", the spire angle, and the height of the spire relative to that of the last whorl and aperture.

In living Toxoglossa the soft anatomy (where known) affords more evidence of the animal's affinities. The morphology of the radula is important in this connexion. The presence or absence of an operculum, and, when present, its structure, are also characters which are generally of taxonomic value only in Recent forms. Fossil gastropods are rarely associated with opercula, even where they are known to have possessed them, and the seeming absence of an operculum in a little-known form is thus without significance.

The **Clinura-Thatcheria** *group*

As mentioned above (p. 262), it was suggested by Beets (1943*b*) that *Clinuropsis*, *Clinura* and *Thatcheria* formed a closely related group. He regarded *Cochlioconus* as part of *Thatcheria*, and did not consider *Waitara* at all. But Powell (1942) had already recognised a relationship between *Waitara* and *Thatcheria* ; and Wenz (1943) placed *Waitara* (at that time known to him only by its Miocene species) near *Clinura*, although he thought that *Thatcheria* and *Cochlioconus* had no affinities with either, or even with each other. Beets, therefore, in a later paper (1951), added *Waitara* to his group.

This suggested grouping has evoked no mention or comment elsewhere. The forms in question certainly seemed to possess some characters in common and no fundamental differences ; in particular, the shell was always more or less pagodiform, with a juxtasutural posterior sinus (admittedly of variable depth) having its vertex close to the suture. All the species seemed to be extremely rare, and were probably abyssal in habit.

More conclusive evidence of this supposed relationship is now available, although the extent of the group requires limitation. Beets' conception of the taxon *Clinura* was a very wide one, even in the more restricted sense in which he used it in 1951. His misunderstanding of the true form of the posterior sinus in the type-species, *C. calliope* (Brocchi), had led him to believe that the depth of the sinus, since it appeared to vary greatly in species which were otherwise similar, was subject to " normal " variation within the group ; yet, in the same work (1943*b* : 364), he stated that the form of the sinus was " ein Merkmal von höchster Bedeutung in der Systematik der Turridae". It has now been made quite clear (see p. 272] that the posterior sinus of the type-species is very deep ; and it is also apparent (see Pl. 47, figs. 3, 6, 8, 11) that its exact shape as found in *C. calliope* is a constant character of *Thatcheria* (including *Cochlioconus*), of *Waitara*, and of certain other species referred to *Clinura* itself, but not of the remaining species hitherto referred to *Clinura* and not of *Clinuropsis*. It is therefore suggested, in accord with Powell and Beets, that the highly distinctive type of sinus found so consistently in these genera is indeed of taxonomic value, notwithstanding what has been written above concerning the variable position and form of the posterior sinus in the Toxoglossa in general. (This, of course, would not be true if a sinus like that of *Thatcheria* could be clearly shown to have developed as a result of parallel evolution in an entirely different group.) It is further suggested that any alleged species of *Clinura* without this deep sinus have been wrongly placed in that genus. An examination of the original descriptions and figures of most of the species mentioned by Cossmann (1896 : 75) ; Grant & Gale (1931 : 494) ; Beets (1943*a* : 296, 297 ; 1943*b* : 358–64) ; Eames (1957 : 51) and Glibert (1960 : 25, 26) indicates that this exclusion from *Clinura* should apply to all the species from North America (Eocene to Miocene), Africa (Palaeocene and Eocene), and the Palaeocene and Eocene of Europe, and to most of those from the Neogene of Europe ; thus it is not possible to agree with Beets that the genera *Clinuropsis* Vincent 1913 (*non* Thiele 1929) and *Nekewis* Stewart 1927 should be placed in the synonymy of *Clinura*. Indeed, the only true species of *Clinura* (using the name in Beets' narrower sense, thus also excluding *Waitara*, *Cochlioconus* and *Thatcheria*) seem to be the type-species and a few others from the Neogene of Europe, together with the two species from the Neogene of Buton (Celebes).

It is noteworthy that the only species (other than *C. calliope*) mentioned by Bellardi when proposing the genus *Clinura* was *C. elegantissima* (Foresti 1868) [*Pleurotoma*], which, by the form of its growth-lines, is clearly not a *Clinura*. Its complex spiral ornament is also very distinctive. On the other hand, a good example of a European species accepted here as a *Clinura* is *C. trochlearis* (M. Hörnes 1854) [*Pleurotoma*]. In the present work, the decision to retain this species within the genus *Clinura* was originally based upon Hörnes' description and figures, with particular reference to the form of the posterior sinus; only later did this decision receive powerful support from the discovery that an individual of *C. trochlearis* in the collections of the British Museum (see p. 274) showed a diagonally cancellate protoconch, just as in *C. calliope*, and transverse, slightly opisthocline costae on the juvenile whorls of the teleoconch. Another species which may be assigned to *Clinura* with a high degree of probability is *C. controversa* (Bellardi 1847) [*Pleurotoma*]; Bellardi, incidentally, ascribed this new specific name to Jan 1845 "in litt. et specim." (p. 64).

More doubtful cases, where it would probably be difficult to make a definite decision on the correct systematic position of the species without handling the actual type-material, include *C. sopronensis* (Wolf 1870) [*Pleurotoma*], *C. subtrochlearis* (Friedberg 1912) [*Surcula*], and *C. sabatiorum* Bellardi 1878. But it is felt that a full examination of every species attributed to *Clinura* by one author or another, often without justification, is beyond the scope of the present review. The species excluded would form such a large and varied assemblage, with such a wide geographical distribution and such a long stratigraphical range, that they would doubtless represent several distinct genera. The available genera to which they might be referred would include those listed by Grant & Gale (1931) and by Beets (1943*b*) as synonyms of *Clinura*, other than *Thatcheria* and *Cochlioconus*: namely, *Clinuropsis* Vincent 1913 (*non* Thiele 1929) and *Nekewis* Stewart 1927. It is possible, however, that not all species might be referred to those or to other existing genera, in which case new genera would be needed.

The Butonese species of *Clinura* are *C. carinata* (Martin 1933) [*Cryptoconus*] and *C. bituminata* (Beets 1943*a*) [*Surculites*].

If the genus *Clinura* be limited as suggested above, which to me seems perfectly reasonable, then the reasons for postulating a close relationship with *Waitara* and *Thatcheria* (including *Cochlioconus*) are much more convincing. But there are no grounds for supposing these forms to be related just as closely to the genus *Clinuropsis*.

Confirmation of this affinity is given by the protoconchs. Until a few years ago that of *Waitara* was the only one described (Powell, 1942). Now, however, the protoconchs of the type-species of *Clinura* and *Thatcheria* have been made known (see p. 274 above; and Kuroda & Habe, 1954); both show the same type of diagonal reticulation, and this suggests a relationship between those two genera. On the other hand, the *Waitara* protoconch described by Powell gives no indication of diagonal cancellation ; but, as stated above, its condition is so unsatisfactory that the nature of its original ornament cannot be ascertained. At least it affords no evidence to refute the suggestion, based on other conchological evidence, that *Waitara* is related to *Clinura* and *Thatcheria*. In any case, the species in question (*Waitara liratula*) is not the type-species of *Waitara*.

Other common characters of the shells, which might be of little taxonomic value on their own, together reinforce the evidence already cited for the relationship of the three genera. They include the pagodiform habit, the distribution of the spiral ornament on the outer surface of the teleoconch, and the smooth, very slightly twisted nature of the columella. The distribution of the spiral ornament cannot always be ascertained very easily from the published descriptions and illustrations ; but the ornament is typically confined to the outer face of each whorl, except in that there are comparatively weak striations on the outer edge of the ramp (next to and parallel with the carina). This type of distribution is certainly found in *Clinura calliope*, *C. trochlearis*, *C. bituminata*, *Waitara pagodula*, *W. liratula*, and in the new species of *Thatcheria* from Fiji described below. In the Recent *Thatcheria mirabilis*, of which the material is of course in a far better state of preservation, the spiral ornament on the ramp extends further towards the adapical suture, but it is altogether fainter than in the other species and is in no way comparable with the much stronger striation of the outer face.

The value of Beets' eventual conclusion, that *Clinuropsis*, *Clinura*, *Waitara* and *Thatcheria* (including *Cochlioconus*) form a closely related group, may therefore be assessed as follows. His suggestion was based at the time on inadequate evidence ; but a more restricted conception of the genus *Clinura*, coupled with better understanding of the form of the posterior sinus in that genus and with new knowledge of the form of the protoconchs in *Clinura* and *Thatcheria*, now indicates that it is perfectly reasonable in so far as *Clinura*, *Waitara* and *Thatcheria* are concerned. *Clinuropsis*, however, does not form part of this group. Further, it cannot be agreed that the similarities between the three named taxa in the group are sufficiently close to justify placing them all in synonymy (senior synonym *Clinura*, ranked as a sub-genus of *Surculites* in Beets, 1943*b*), or even to warrant their being considered as three separate sub-genera of *Surculites* (in Beets, 1951). In the following argument they are regarded initially as three distinct genera. In any case, close affinity with *Surculites* is denied in the present work ; the matter is discussed more fully below (p. 289), where the external relationships of the *Clinura-Thatcheria* group are considered in detail.

At present, then, this group appears to include at least the following species :

Clinura calliope
C. trochlearis
C. controversa
C. bituminata
C. carinata

Waitara waitaraensis
W. generosa
W. pagodula
Waitara sp. nov. Powell 1942 aff. *pagodula*
W. liratula

Thatcheria mirabilis
T. gradata
Thatcheria sp. nov. Beets 1951

Division into genera

The species referred to *Waitara* seem, in general, to be intermediate in character between *Clinura* and *Thatcheria.* This division of the group into three genera, however, appears rather unsatisfactory : like species are separated (*C. carinata* and *W. pagodula, W. liratula* and *T. mirabilis*) and unlike species placed together (*C. bituminata* and *C. carinata, W. generosa* and *W. liratula*). A careful consideration of all the species involved has led to the following conclusions.

All three species listed as *Thatcheria* are correctly regarded as congeneric with each other. But several other species listed above (*Clinura carinata, Waitara pagodula, Waitara* sp. nov. Powell 1942 aff. *pagodula, W. liratula*) and the new species from Fiji described below as *Thatcheria vitiensis* are all very similar to the three species of *Thatcheria* listed ; they resemble them in having the carina generally high on the larger whorls and only weak spiral ornament, and in being entirely free of transverse ribbing or tubercles at every stage of development (except, in three cases, for minute vestigial nodules on the very youngest whorls of the teleoconch), while they differ from them chiefly in being less pagodiform. Indeed, there is little more than the variable degree of pagodiformity to distinguish any of these eight species from each other. It is therefore suggested that they should all be placed in the genus *Thatcheria.*

The geographical distribution of the genus as thus enlarged remains entirely within the area of the Western Pacific. Its stratigraphical range extends from Upper Miocene to Recent, but it is predominantly Pliocene.

Powell (1942), of course, recognised the affinity of *Waitara* and *Thatcheria* (see pp. 260,261), " probably basing his opinion mainly on the features of two species of *Waitara* newly described by him " (Beets, 1951 : 16). But, because he had misinterpreted the form of the posterior sinus of *T. mirabilis* from the growth-lines shown in Angas' rather misleading figure, he doubtfully retained *Waitara* as a separate genus " for New Zealand usage ". Beets (1951 : 16) pointed out that the sinus in *T. gradata* [*Cochlioconus*] " is almost similar to that in *Waitara* ", but he failed to realise Powell's mistake in the matter of the *T. mirabilis* sinus, even though he himself had earlier figured it correctly (1943*b*, pl. 36, fig. 2). However, this misinterpretation has now been explained (pp. 269, 270) ; and Powell's younger species of *Waitara* (though not Marwick's two older species, one of which is the type-species) have been referred to *Thatcheria.*

On the other hand, if it should later transpire that the protoconch of *T. liratula* and its allies (known in only the one specimen of *T. liratula,* which seems to have been subsequently damaged) is, as appears from Powell's description and figure, essentially different from that of *Thatcheria,* then it would be necessary to erect a new genus for those forms.

If the younger species formerly ascribed to *Waitara* are transferred to *Thatcheria,* then the only species remaining in the former genus are the type-species *waitaraensis,* from the Upper Miocene of New Zealand, and *generosa,* from the Lower Miocene of the same country. Marwick's fairly detailed generic diagnosis of *Waitara* appears to be based equally upon *waitaraensis* and *generosa,* so that, as mentioned above (p. 261), Wenz (1943) was misled into believing that *generosa* was the type-species of the genus. But, as far as can be judged from Marwick's descriptions of these two species, only one individual is known of each. The holotype of *waitaraensis* in particular is very incomplete and seems to have suffered distortion ; there are no highly distinctive characters, either positive or negative. It therefore seems that the genus *Waitara*, defined objectively by reference to this single specimen, cannot be defined very clearly. It is nevertheless obvious from Marwick's descriptions and figures that, unlike *W. pagodula* and *W. liratula*, neither *W. waitaraensis* nor *W. generosa* can be referred to *Thatcheria*. Neither species is much less pagodiform than is *T. liratula* or the new Fijian species *T. vitiensis*—indeed, they are probably more pagodiform than is *T. pagodula*—but their whorls have an entirely different aspect.

On the other hand, Beets wrote (1951 : 16) that " there are also relationships between *Waitara* in its former sense (i.e., as based upon *W. generosa* and *W. waitaraensis*) and *Clinura* ". This appears to be true at least of *W. generosa*, which has both the characteristic attributes of a *Clinura* : the first few whorls of the teleoconch are ribbed, with tubercles on the carina, and the carina is low on the larger whorls (that is, the ramp slopes steeply downwards). These show its affinity with the European species of *Clinura* (including the type-species, *C. calliope*) and with the Butonese *C. bituminata*. It is therefore proposed that *W. generosa* be transferred to the genus *Clinura*. As for *W. waitaraensis*, the incomplete and distorted nature of the specimen prevents its giving any information on these characters ; but, since Marwick (who handled the material) believed it to be congeneric with *W. generosa*, it may also be transferred—albeit provisionally—to *Clinura*, thus making *Waitara* a subjective junior synonym of *Clinura*. If better material later showed that this transfer, though correct for *W. generosa*, was not justified in the case of *W. waitaraensis*, the generic name *Waitara* would still be available for the latter species.

The genus *Clinura*, as listed above, has now lost *C. carinata* to *Thatcheria* but has gained the species *waitaraensis* and *generosa* from *Waitara* ; i.e., it includes the species *calliope*, *trochlearis*, *controversa*, *bituminata*, *generosa*, perhaps *waitaraensis*, and possibly others from Europe. The geographical distribution of the genus in this new sense is thus restricted to Europe (the Mediterranean Basin), the East Indies and New Zealand. The European species are all of Miocene age, although some (such as *C. calliope* itself) persist into the Lower Pliocene (Plaisancian) ; the Butonese species is of Neogene age, very probably Upper Miocene ; and the two New Zealand species, as mentioned above, are from the Lower and Upper Miocene respectively. It may therefore be said that the stratigraphical range of *Clinura* is from the Lower Miocene to the Lower Pliocene, but that the genus occurs mainly in the Middle and Upper Miocene.

The stratigraphical range of *Clinura* contrasts with that of *Thatcheria*, essentially Pliocene to Recent. This shows that the most natural break in the *Clinura-Thatcheria* group occurs between the earlier and the later species of " *Waitara* " at about the level of the Miocene-Pliocene boundary. It seems, however, that there is a certain amount of overlap on either side of that boundary. In one direction *C. calliope* survives into the Plaisancian, as do other possible species of the genus (see Glibert, 1960 : 25, 26) ; in the other, rocks which are probably no younger than

Upper Miocene already contain *T. carinata*, and *T. pagodula* may likewise be of Upper Miocene age.

The genus *Clinura*, even in the restricted sense used here, cannot be defined very easily ; it is essentially a rather variable assemblage of species, of wide distribution and of predominantly Miocene age. *Thatcheria*, on the other hand, even in the present broad interpretation, is a fairly homogeneous group of species and may be defined quite clearly. It seems that it originated from *Clinura* towards the end of the Miocene, became widespread in the Western Pacific area during the Pliocene, and survives to the present day as the one rather " extreme " form living in deep waters off the Japanese coast.

T. mirabilis may in fact occur more widely than is known at present, " off Japan " ; for a rare abyssal form is far more likely to be recovered in the Kii region, off the south coasts of Honshu and Shikoku, than anywhere else in the Pacific. Not only is the Pacific Ocean almost at its deepest off Japan, but in few places are there such deep waters so near to a large area of land. Indeed, they are nowhere else so close to a heavily populated shore-line from which intensive fishing is carried out.

Interspecific differentiation in **Thatcheria**

The eight species referred in this work to the genus *Thatcheria* seem to differ from each other in little more than in certain characters of the spire : in its degree of pagodiformity, in its acuteness, and in its size relative to that of the last whorl and the aperture. In general, the various species seem to form an evolutionary series in which the degree of pagodiformity increases with time ; and, as it increases, the spire appears less acute.

It is very difficult, if not impossible, to define " pagodiformity " objectively. Several numerical properties of pagodiform shells were examined as possible indices but rejected for various reasons ; they are shown in Text-fig. 8. Measurement of the spire angle proved more useful, for this, in a shell of the type under consideration, can be measured in two different ways (Text-fig. 9). The term " internal spire angle " may be introduced for the angle between the two lines which, on either side of the spire, connect the intersections of the suture with the lateral profile. It is obvious that only an approximate value can be obtained for this, for the lines are unlikely to be straight ; it is not even likely that smooth continuous curves can be drawn to pass exactly through all the points, and the best that can be obtained will nearly always be a slightly concave curve passing close to most of them. The " external spire angle " is measured in a similar manner but is based on the intersections of the carina with the lateral profile ; it is, of course, larger than the internal spire angle.

Of the eight species of *Thatcheria* in which such measurements were possible (including *T. vitiensis* sp. nov. described below), seven gave a value for the internal spire angle which was remarkably constant, lying always between 38° and 46° ; exact measurements would not be especially significant, for, even in different individuals of one species (the Recent *T. mirabilis*), the angle varied between 38° and 44°. Only *T. pagodula* gave a significantly different value, 57°.

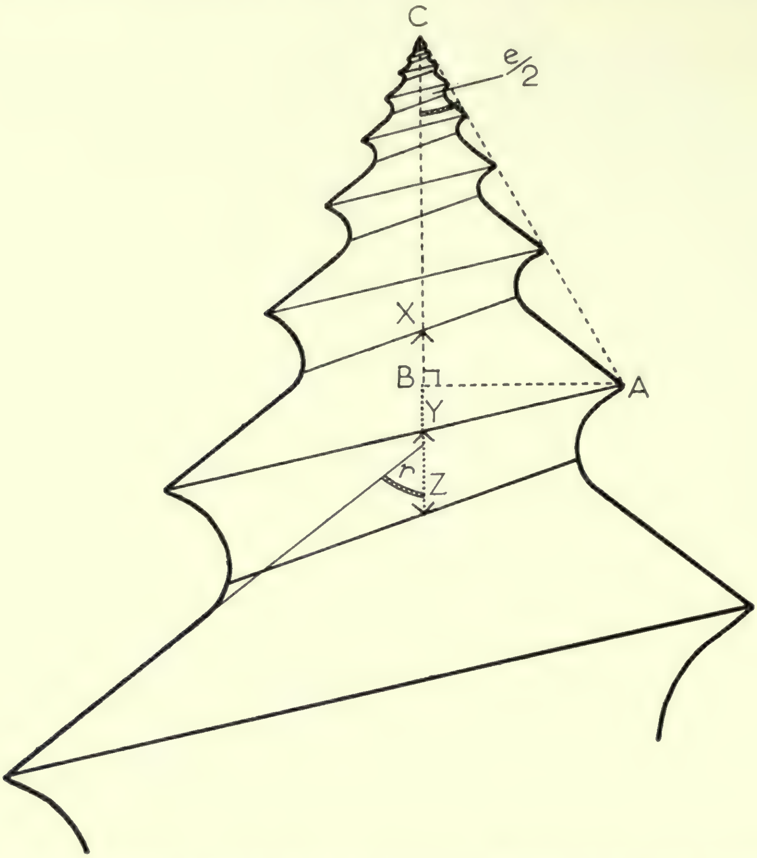


FIG. 8.—Plane projection of the spire of an idealised pagodiform shell, to illustrate the numerical properties examined as possible indices of pagodiformity but rejected for various reasons. They are :

(*a*) The projection of the carina, expressed as the ratio of its perpendicular distance from the shell axis (AB) to the distance of that perpendicular from the apex (BC). This is the tangent of half the external spire angle (*e*).

(*b*) The angle (*r*) between the profile of the ramp and the shell axis.

(*c*) The height of the carina on the whorl, expressed as the ratio of its axial distance from the lower suture (YZ) to the axial distance between the sutures (XZ).

On the other hand, the external spire angle varied greatly, from 50° in the earliest species *T. carinata* to 82° in the holotype of the Recent *T. mirabilis*. It seemed to show a fairly steady increase with the passage of time ; but *T. pagodula* was once again the exception, with an external spire angle of 71°. This higher value, however, is consistent with the higher value for the internal spire angle. In fact, the ratio of the external spire angle to the internal, which might be called the " index of pagodiformity ", is the same in *T. pagodula* as in the much slimmer *T. carinata* (the only other species of possibly Miocene age)—namely, 1.25.

To sum up, then, the situation seems to be that there are two species of *Thatcheria* of possibly Miocene age. One of these (*T. carinata*) has an internal spire angle of

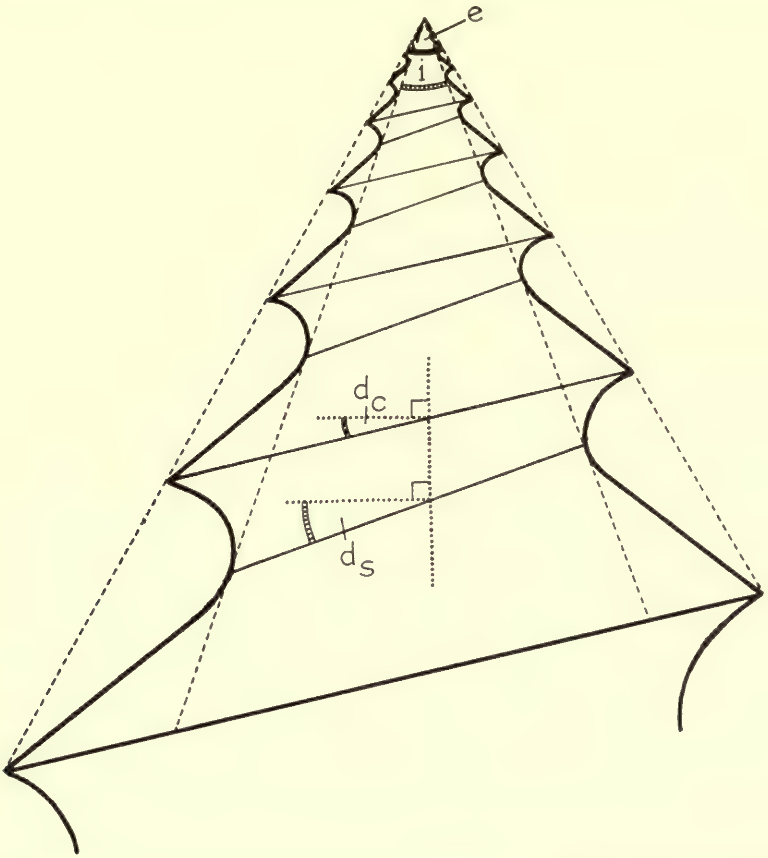


FIG. 9.—Plane projection of the spire of an idealised pagodiform shell, to illustrate:
i—the internal spire angle,
e—the external spire angle,
d_s—the angle of declination of the suture, and
d_c—the angle of declination of the carina.

Note:

(*a*) d_s is greater than d_c in a pagodiform shell, for the suture descends in a tighter (and therefore steeper) spiral than does the carina.

(*b*) Both d_c and d_s are smaller than they appear in the plane projection. This is because, in the plane projection, both carina and suture appear to descend from one side of the shell to the other in a straight line; whereas, in fact, they do so on the surface of a cone and therefore less steeply.

(*c*) $\frac{\tan d_s}{\tan d_c}$ should be equal to $\frac{\tan e/2}{\tan i/2}$.

40°, the other (*T. pagodula*) has a much broader spire (internal spire angle 57°); but both have exactly the same index of pagodiformity (1·25). All the later species have an internal spire angle which is much the same as in *T. carinata*; but the index of pagodiformity, like the external spire angle, shows an increase with the passage of time—to 1·50 in the two supposed Lower Pliocene species (*T. liratula*, *T. vitiensis*), to 1·58–1·62 in the two species described simply as "Pliocene" (*T.*

gradata, Thatcheria sp. nov. Beets 1951), and to 1·75–2·05 in the Recent *T. mirabilis.*

It seems likely that the index of pagodiformity will prove to be more constant and characteristic for a given species than either the internal or external spire angle; for the two spire angles, though they may vary considerably between individuals, seem to do so together. Use of the index, though liable to considerable error, may afford a rough indication of the course of evolution.

Of course, the position of a species on the evolutionary scale (and hence its approximate geological age) should not be assessed on any one character alone. The various characters probably evolved at different rates in different lineages.

Evolution in the **Clinura-Thatcheria** *group*

Clinura calliope, type-species of the genus *Clinura,* ranged from Upper Miocene to Lower Pliocene. *Clinura,* however, was already well diversified at the beginning of that time; thus the type-species occurred too late to occupy any central position in the phylogeny of the genus as defined in the present work. Moreover, in one prominent feature *C. calliope* differs from the other species which are considered here to constitute that genus: the entire carina is furnished with well developed tubercles.

A better claim to a central position may be made on behalf of *C. trochlearis* (from the Middle Miocene[1] of Europe). Unlike every other species referred to *Clinura, C. trochlearis* may be placed in that genus with absolute certainty. Except for the poorly known, rather peculiar *C. generosa* in the Lower Miocene, it is probably the oldest species of *Clinura.* It is somewhat variable in form, especially with regard to the acuteness of the spire and the position of the carina on the whorl. And it is also the most " central " in form; for it could well be ancestral, by a late Miocene radiation, to all the Upper Miocene species of *Clinura* and to *Thatcheria.*

Of those species in the Upper Miocene, *C. waitaraensis* is rather like *C. bituminata* in the general aspect of its whorls, which, where undamaged, seem to have a steeply inclined ramp and a low carina; further, both those species are very similar to *C. trochlearis. C. bituminata* and *C. waitaraensis* could be derived from a common ancestor which, in turn, had evolved from *C. trochlearis* with little change in form. Migration from Europe to the south-western Pacific would have occurred at the onset of this hypothetical evolution.

Another species in the Upper Miocene of the south-western Pacific which also is similar to *Clinura trochlearis* is *Thatcheria carinata*; the flatter ramp and higher carina distinguish it from *C. bituminata* and *C. waitaraensis.* Like those two species, *T. carinata* may have been derived from a migrating descendant of *Clinura trochlearis.* From *Thatcheria carinata* a line of evolution to the Recent *T. mirabilis* may be envisaged; it has been shown above that, with passage of time, the internal spire angle remained more or less constant while the external spire angle (and hence the index of pagodiformity) gradually increased. Only *T. pagodula,* with its generally much stouter spire, would necessarily have formed a distinct Upper Miocene offshoot from this series. It also seems that the evolution of *Thatcheria* from

---

[1] Some authorities now prefer to regard the Zweite Mediterran-Stufe (Suess, 1866) of the Vienna Basin as Tortonian in age, i.e. Upper Miocene, rather than Helvetian. But *C. trochlearis* occurs also in the Middle Miocene of Italy (Bellardi, 1877 : 206).

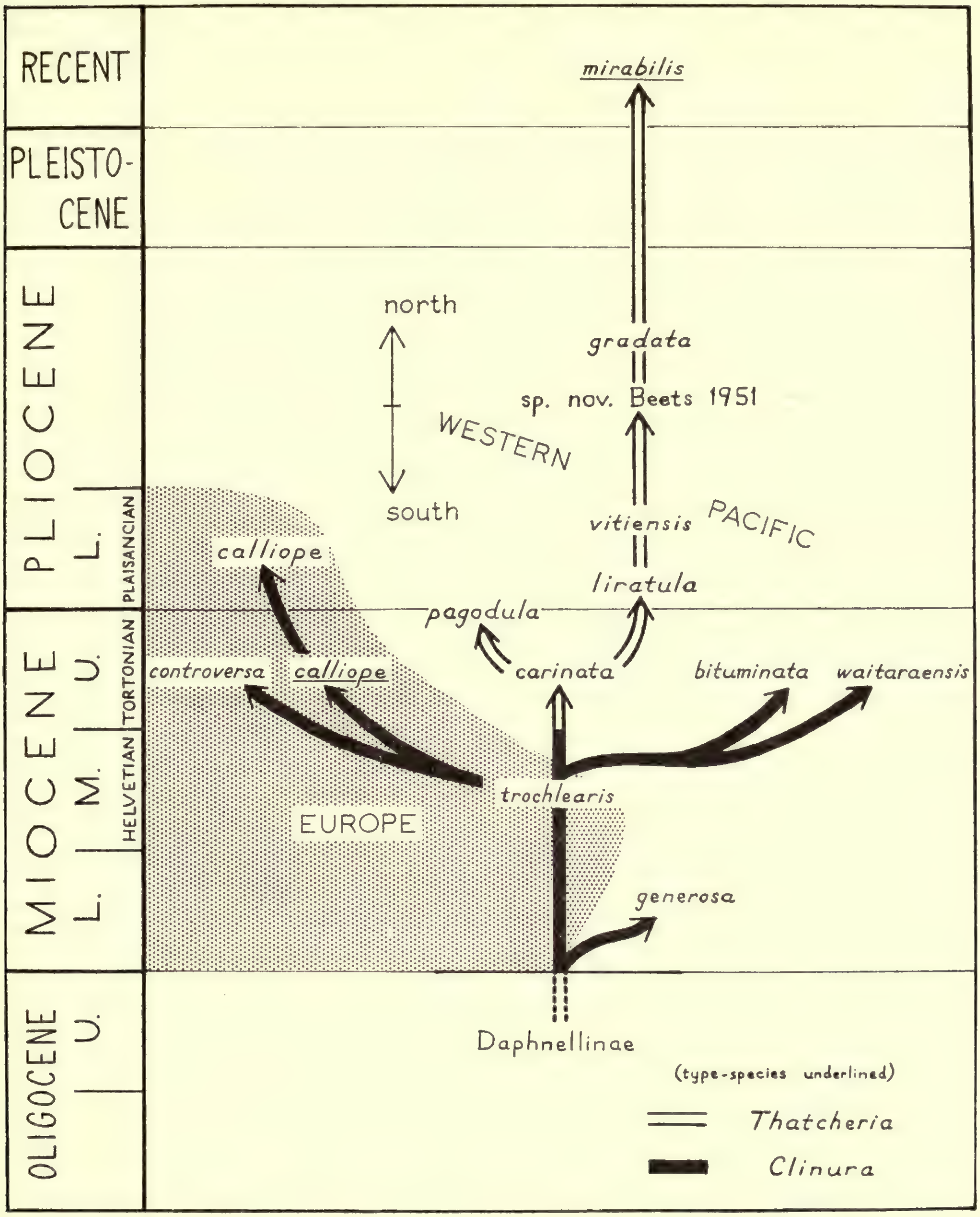

RECENT
PLEISTOCENE
PLIOCENE
L.
PLAISANCIAN
MIOCENE
U.
M.
L.
TORTONIAN
HELVETIAN
OLIGOCENE
U.
mirabilis
north
south
WESTERN PACIFIC
gradata
sp. nov. Beets 1951
vitiensis
liratula
calliope
pagodula
controversa
calliope
carinata
bituminata
waitaraensis
trochlearis
EUROPE
generosa
Daphnellinae
(type-species underlined)
Thatcheria
Clinura

FIG. 10.—A very tentative evolutionary tree of the Thatcheriinae.

the Miocene onwards has been accompanied by a northward movement of the population towards its present home in the north-western Pacific.

The only other species in the Upper Miocene which have definitely been referred to *Clinura* are both from the Mediterranean region, *C. calliope* (the type-species, persisting into the Lower Pliocene) and *C. controversa*. A list of characters distinguishing these two species (at that time referred to *Pleurotoma*) was drawn up by Bellardi (1847 : 64); in fact, it was largely by means of this comparison with *P. calliope* that he described his new species *P. controversa*. Once again *C. trochlearis* may be regarded as a possible ancestor—of *C. calliope*, *C. controversa*, or both,—but in this case there is no need to postulate a distant migration of the stock. The tendency towards the development of transverse sculpture on the first few whorls of the teleoconch, manifested in *C. trochlearis* and in other early species of the group, might have led to the evolution of *C. calliope* by affecting the whole shell; and, in similar fashion, *C. controversa* might have evolved through the development of a notched carina.

As for *Clinura generosa* in the Lower Miocene, this species has a somewhat different appearance; it is difficult to imagine it as a direct ancestor of *C. trochlearis* and of all the other species mentioned. But it has the typical posterior sinus of the *Clinura-Thatcheria* group, together with the tubercles on the early whorls of the teleoconch. It must therefore be retained within the group, in the genus *Clinura*, and placed on a sterile side-branch of the evolutionary tree.

All these suggestions are summarised in Text-fig. 10.

Systematic position of the **Clinura-Thatcheria** *group*

Serious consideration of *Thatcheria* and its relatives has led most modern authors to place them in the Turridae (Eales, 1938; Beets, 1943*b*, 1951; Kuroda & Habe, 1954, implicitly; Habe, 1955). There have been only two important exceptions. Yokoyama (1928, 1930), though he did not explicitly refer *Thatcheria* [*Cochlioconus*] to the Conidae, thought it had affinities therewith; while Powell (1942) regarded *Waitara*, *Cochlioconus* and *Thatcheria* as constituting a new family, the Thatcheriidae, distinct from the Turridae (though parallel to them) and more closely related to the Conidae.

Preference is given here to the view that this group of gastropods is best placed in the Turridae. The posterior sinuses of *Clinura* and *Thatcheria* may indeed be compared with those of certain Conidae (e.g., *Conus araneosus* Solander 1768); although, in general, the outer lip is drawn further forward in *Clinura* and *Thatcheria* before it crosses the line of the carina. On the other hand, their posterior sinuses also resemble those of certain turrids; the diagonally cancellate ornament on the protoconchs of *Clinura* and *Thatcheria* is a turrid character; and neither genus is known to show any manifestation of the tendency, typical of the Conidae, to resorb the columella and early internal walls. Further, the form of the radula in *Thatcheria mirabilis* and other characters of that Recent species confirm the opinion that the group should be referred to the Turridae, particular significance being attached to Eales' work upon the soft anatomy. There would seem to be little or no justification for the erection of a separate family to accommodate *Clinura* and *Thatcheria*, even if that family should be considered as having turrid rather than conid affinities.

Clinura, of course, had been placed in the Turridae (Pleurotomidae) from the very date of its establishment in 1875, long before Eales (1938) wrote her paper on *Thatcheria* and long before it was first suggested that the two genera were related. A brief history of the more exact classification of *Clinura* has already been given above (pp. 263–268); sufficient here to note that, of recent years (since 1931), the taxon has been generally regarded as a sub-genus of *Surculites*. Grant & Gale wrote (1931 : 494) :

" *Clinura* is closely related to *Turricula*, and might be considered a variational extreme in the opposite direction from *Pleurofusia*. It can, however, be distinguished generically by its shorter form and broad, shallow notch. It is even more closely related to *Surculites* proper, *Pseudotoma*, and *Megasurcula*, sharing with them the broad conical shape and wide shallow notch, so that it is here not separated from them generically. . . . It probably was derived from *Turricula*, perhaps indirectly, and later gave rise to, or is a branch of the stock that gave rise to, *Pseudotoma* and *Megasurcula*. The intergradations between it and the last named are evident in the California and Washington Tertiary. *Clinura* and typical *Surculites* are both well represented in the Eocene of the Pacific coast, . . . *Clinura* lived on into the Miocene, where it is represented by [*Megasurcula*] *keepi* (Arnold), . . . "
It is clear from this, however, that Grant & Gale were basing their arguments largely upon the characters of the species in the Eocene of North America which they had referred to *Clinura* ; and those species, as pointed out above, do not possess the deep posterior sinus which is considered here to be the most essential character of the genus. Their opinions, therefore, do not apply to *Clinura* in its proper sense.

But, in any case, Wrigley (1939 : 282, 283) recognised quite correctly that the genus *Surculites* was not a turrid, having no true sinus or notch like that of the typical members of the family. He concluded that " The sinuous growth lines [of *Surculites*] here considered are not an unequivocal mark of the Turridae, they may occur in other families, linked with and proportionate to whorl-carination. *Surculites* is long extinct, we have no guidance from the animal anatomy and, in the light of the foregoing comparisons, it seems best to place the genus in a not too determinate position between the Fusinidae and the Buccinidae . . . " On the other hand, he also noted that " *Surculites* has some resemblance, especially in general form, to *Clinura* Bellardi, but in that genus the growth lines sweep back over the rear slope four or five times as far as those of *Surculites*, here showing a Turrid character, or rather, a contour often seen in the Conidae." Thus, if the species properly referred to *Clinura* have no affinity with *Surculites*, then *Clinura* may be a turrid even though *Surculites* is not. Further, this means that *Clinura* cannot be regarded as a sub-genus of *Surculites* (in which classification Grant & Gale (1931) were followed by Beets (1943*a*, 1943*b*, 1951)), nor can *Thatcheria* be considered as part of the latter genus (as in Beets, 1943*b*, 1951).

The true characters of *Clinura* and *Thatcheria* not only link those genera with the Turridae but with a particular sub-family thereof, the Daphnellinae. Of all the turrid sub-families listed by Powell (1942 : 29), only the Daphnellinae have (sometimes) a diagonally cancellate protoconch (see Text-fig. 7) ; only the Daphnellinae possess a juxtasutural posterior sinus ; only the Daphnellinae and the Mangeliinae, together with a few genera in other sub-families, lack an operculum ; and the radula of the Daphnellinae, which has marginal teeth only, is very similar to that of *Thatcheria*. Indeed, Kuroda & Habe wrote of *Thatcheria mirabilis* (1954 : 81) that the protoconch " shows the obliquely reticulated texture of sculpture, suggesting that it is also of a Daphnelloid ", and (p. 80) that the species has a radula, " whose peculiar shape shows that it has a close affinity with the Daphnellinae".

But Powell (1942 : 167) had two objections to the location of *Thatcheria* and its allies in the Daphnellinae, " the lack of a typical Daphnellid apex . . . and the actual form of the sinus ". It has already been shown that the only *Thatcheria* protoconch known at that time, that of *T. liratula* [*Waitara*], was so badly abraded as to be useless ; but Powell was correct in supposing that the form of the *Thatcheria* sinus (either as he wrongly believed it to be in *T. mirabilis*, having been misled by Sowerby's figure to Angas' description, or as he actually observed it in *T. liratula*) was not quite like that of the Daphnellinae. The other differences between the Daphnellinae on the one hand and *Clinura* and *Thatcheria* on the other (listed below in Table II) cannot preclude the possibility that the *Clinura-Thatcheria* group originated from the Daphnellinae in the Upper Oligocene or Lower Miocene by the development of a larger, pagodiform shell ; even the protoconchs of *Clinura* and *Thatcheria*, now known from one good specimen of each of three species (*C. calliope, C. trochlearis, T. mirabilis*), agree with such a theory. But, from the taxonomic viewpoint, the consistent difference between the groups in the form of the posterior sinus is more fundamental. All things considered, it seems that, while *Clinura* and *Thatcheria* should be placed in the Turridae and may well have evolved from the Daphnellinae, they form a group which is so distinctive that it is best not to regard it as part of the Daphnellinae.

TABLE II

	Daphnellinae	*Clinura* and *Thatcheria*
Form of posterior sinus (juxtasutural)	Typically a " reversed L "	Smoothly arcuate, with outer lip drawn far forward
Protoconch (see Text-figs. 3–7)	Generally diagonally cancellate ; but never exactly like that of *Clinura* and *Thatcheria*	Diagonally cancellate (where adequately known)
Spire	Rarely pagodiform, if ever	Always more or less pagodiform
Whole shell . . .	Generally small	Always fairly large
Earliest known occurrence .	Oligocene, perhaps even Cretaceous	Lower Miocene
Present trend . . .	Still increasing	Seemingly tending towards extinction

The only logical alternative is to erect for them a special sub-family within the Turridae, the Thatcheriinae; i.e., it is proposed that the family Thatcheriidae Powell should be reduced in rank and the name of the taxon amended accordingly. The Thatcheriinae have a particularly close relationship with the Daphnellinae. The pagodiform habit, so characteristic of the former sub-family (especially its later members), has been evolved in a very similar manner in other sub-families of the Turridae, e.g. in the Cochlespirinae (compare *Leucosyrinx* (*Aforia*) *circinata minatoensis* Otuka 1949, pl. 13, fig. 11, from the Pliocene of Japan) ; but the Thatcheriinae may be easily distinguished from such parallel developments by the form of the posterior sinus.

Formal classification

Family TURRIDAE

Sub-family THATCHERIINAE Powell 1942 nom. transl. herein

Shell generally fairly large. Spire short relative to size of last whorl, very slightly coeloconoid, more or less pagodiform with deep suture and well developed carina. Posterior sinus on ramp of last whorl, juxtasutural, rounded, with vertex close to suture and deepened by forward extension of outer lip ; outer lip simple and slightly convex between carina and anterior canal ; distinct collabral growth-lines developed accordingly on ramp and outer face of whole teleoconch. Protoconch diagonally cancellate. Spiral ornament on outer face of teleoconch, and usually on outer edge of ramp next to carina ; transverse sculpture may be present on juvenile whorls of teleoconch (sometimes also on adult whorls), generally leading to formation of tubercles or notches on carina, but, alternatively, it may be entirely absent. Columella smooth, very slightly twisted. Operculum unknown and probably absent ; soft anatomy of the only Recent species typically turrid ; radula of that species like that of the Daphnellinae, with one pair of marginal teeth and no others.

OCCURRENCE. Lower Miocene to Recent ; Mediterranean Basin and Western Pacific.

Genus ***CLINURA*** Bellardi 1875

?[1931. *Waitara* Marwick, p. 149.]

DIAGNOSIS. Spire slightly or moderately pagodiform with carina generally nearer to abapical suture ; juvenile whorls of teleoconch (sometimes also adult whorls) bear transverse sculpture, generally leading to formation of tubercles or notches on carina ; spiral ornament usually well developed.

TYPE-SPECIES. *Murex calliope* Brocchi 1814 by subsequent designation of Bellardi, 1877. Upper Miocene to Lower Pliocene ; Italy and Southern France.

RANGE. Lower Miocene to Lower Pliocene (mainly Middle and Upper Miocene) ; Europe, East Indies, New Zealand.

REFERRED SPECIES. *C. generosa* (Marwick 1931) [*Waitara*] ; Lower Miocene, New Zealand.

C. trochlearis (M. Hörnes 1854) [*Pleurotoma*] ; Middle Miocene, Vienna Basin and Italy.

C. controversa (Bellardi 1847) [*Pleurotoma*] ; Upper Miocene, Italy.

C. bituminata (Beets 1943) [*Surculites*] ; Upper Miocene, Buton (Celebes).

SPECIES REFERRED PROVISIONALLY. *C. waitaraensis* (Marwick 1926) [*Turricula*] ; Upper Miocene, New Zealand. (May still represent distinct genus *Waitara* Marwick 1931.)

[*Clinura* may also include :

C. sopronensis (Wolf 1870) [*Pleurotoma*] ; Upper Miocene, Vienna Basin.

C. subtrochlearis (Friedberg 1912) [*Surcula*] ; Upper Miocene, Poland,

C. sabatiorum Bellardi 1877 ; Lower Pliocene, Italy.

Other species from the Miocene and Lower Pliocene of Europe.]

Genus **THATCHERIA** Angas 1877

1928. *Cochlioconus* Yokoyama, p. 338.

Diagnosis. Spire moderately to extremely pagodiform, with carina generally nearer to adapical suture; no transverse ribbing, no tubercles or notches on carina (except for minute nodules on apical whorls of teleoconch in earlier forms); spiral ornament usually weak.

Type-species. *Thatcheria mirabilis* Angas 1877 by monotypy. Recent; off Japan.

Range. Upper Miocene to Recent (mainly Pliocene); Western Pacific (New Zealand, Fiji, East Indies, Japan).

Referred species. *T. carinata* (Martin 1933) [*Cryptoconus*]; Upper Miocene, Buton (Celebes).

T. pagodula (Powell 1942) [*Waitara*]; Upper Miocene or Lower Pliocene, New Zealand.

Thatcheria sp. nov. aff. *pagodula* (Powell 1942) [*Waitara*]; Lower Pliocene, New Zealand.

T. liratula (Powell 1942) [*Waitara*]; Lower Pliocene, New Zealand.

T. vitiensis sp. nov. (see below); Lower Pliocene, Fiji.

Thatcheria sp. nov. Beets 1951; Pliocene, East Borneo.

T. gradata (Yokoyama 1928) [*Cochlioconus*]; Pliocene, Japan.

T. cf. *gradata* (Yokoyama 1928) MacNeil 1960; Pliocene (and Upper Miocene?), Okinawa.

VII. A NEW SPECIES OF *THATCHERIA* FROM THE PLIOCENE OF FIJI

Thatcheria vitiensis sp. nov.

Pl. 47, figs. 4–6

Derivation of Name. Viti—the Fijian name for Fiji.

Diagnosis. A species of *Thatcheria* with a fairly thick shell, a relatively long and slender spire and a moderately projecting carina. The whorls bear dense, distinct spiral ornament on the outer face and a few weaker spiral striations on the outer part of the ramp. The first few whorls of the teleoconch bear minute nodules on the carina.

Holotype. The unique specimen, Brit. Mus. (Nat. Hist.) Palaeont. Dept. no. G. 91124 (collector's field number VL. 1); it lacks the extreme apex of the spire, the outer lip and the anterior canal.

Occurrence. In tuffaceous marls of the Vanua Levu Formation, of probable Lower Pliocene age. On the new south coast road near Savusavu, Eastern Vanua Levu, Fiji; a large breast-cut 4 miles east of Salt Lake point where the road crosses higher ground north of Naweni.

Description.

[*Note.* (1) The protoconch is entirely lacking, and the condition of the early whorls is poor. (2) Although the whole of the outer lip has been broken off, the ramp of the last whorl is preserved up to its end. Had it extended further, it would surely have left some indication of its attachment to the outer face; and, in any case, the end of the suture is coincident with the adapical end of the last striation marking the limit of growth of the inner part of the mantle. (3) The abapical end of the shell is also missing, but may be reconstructed with a fair degree of probability by reference to *T. mirabilis*. (4) The surface of the shell is abraded, but only very slightly.]

MEASUREMENTS.

Length as preserved	45 mm.
Estimated total length	51 mm.
Height of spire as preserved	22 mm.
Estimated total height of spire	23 mm.
Estimated height of last whorl	34 mm.
Maximum diameter (from end of carina to point diametrically opposite on carina of last whorl)	26 mm.
Internal spire angle	38°
External spire angle	57°
Angle of declination of suture (from plane perpendicular to shell axis) (see Text-fig. 9)	14°
Angle of declination of carina (see Text-fig. 9)	8°

This species shows a less extreme development of the characteristic form of the type-species (*T. mirabilis*). The shell is rather thick and solid; this applies especially to the carina, the outer part of the ramp adjacent thereto, the columella, and the outer lip in the region of the anterior canal. The internal spire angle is a little less than in other species of the genus, the external spire angle much less than in any other species except the Miocene *T. carinata*; the index of pagodiformity is greater than in *T. carinata* or the much stouter *T. pagodula*, about the same as in the slightly stouter *T. liratula*, and less than in the other species. The height of the spire is about 80% of the estimated height of the aperture; the corresponding figure for *T. liratula* is about 50% (*fide* Powell) and for *T. mirabilis* 57%.

The whorl profile shows that the carina projects rather acutely; in the younger whorls both the outer face and the ramp are appreciably concave, the outer face being directed steeply downwards. On the penultimate and last whorls, however, the outer face shows a more or less straight profile; and the ramp of the last whorl has a very marked angular concavity, the angle lying rather nearer to the suture than to the carina.

The spiral ornament is very much like that of *T. liratula* and is clearly shown in Plate 47, figs. 4–6; the striations pass further into the interior of the last whorl, beyond the inner lip, than they do in *T. mirabilis*. There are very faint indications of minute nodules on the carina of the earliest whorls, just as in *T. liratula*. The growth-lines are also like those of *T. liratula*, the parts on the ramp showing that the characteristic posterior sinus of the Thatcheriinae was present; the parts on the outer face, however, are inclined much less obliquely to the shell axis than they are in the New Zealand species. One peculiarity of the holotype, if not of the species, is the series of undulating striations on the inner lip which mark the limit of growth of the inner part of the mantle.

REMARKS. This species is closely related to *Thatcheria liratula* (Powell), to which it has an especial resemblance in its degree of pagodiformity, in the type and distribution of the spiral ornament, and in the presence of minute nodules on the first few whorls of the teleoconch. It may be distinguished from *T. liratula*, however, by its more acute spire, which is much longer relative to the aperture ; by the less oblique growth-lines on the outer face ; and by the fact that its carina is rather more acute, with the result that both the ramp and the outer face of each whorl generally appear a little more concave.

T. liratula is from the Opoitian (Lower Pliocene) of New Zealand. The resemblance of *T. vitiensis* to *T. liratula* rather than to any other species tends to confirm the suspected Lower Pliocene age of the marls from which *T. vitiensis* was collected.

T. vitiensis is also like the Okinawan form which MacNeil (1960) described as *T.* cf. *gradata*, and which, as pointed out above, seems to have a close affinity with *T. liratula*. The Okinawan shell, however, differs from the Fijian species in certain details. The carina appears to be rather higher on the whorl and to project further, producing an almost flat ramp and a more pagodiform spire (just as in *T. gradata* itself, from Japan) ; while the nodules on the carina of the early whorls of the teleoconch, if not better developed, are at least much better preserved than in *T. vitiensis*.

ASSOCIATED FAUNA. Four other shells (three gastropods and one lamellibranch) were found in the Vanua Levu Formation with *Thatcheria vitiensis*. They will be described elsewhere.

VIII. ACKNOWLEDGMENTS

The specimen described above as the holotype of *Thatcheria vitiensis* sp. nov. was collected by Mr. R. W. Bartholomew of the Fiji Geological Survey Department, and was sent to London for examination by permission of Dr. N. J. Guest, Chief Geologist. Their interest and encouragement are gratefully acknowledged.

My especial gratitude is due to Dr. L. R. Cox, F.R.S., for all the help he so patiently gave me. Among the many others who kindly offered useful information, suggestions and criticism were Dr. C. Beets, Mr. S. P. Dance, Dr. N. B. Eales, Mr. C. Matheson, Prof. J. E. Morton, Mr. C. P. Nuttall, Dr. A. W. B. Powell, Mr. E. P. Smith, Mr. F. M. Wonnacott, and, in particular, Mr. D. L. F. Sealy.

Dr. C. A. Fleming, Chief Palaeontologist to the New Zealand Geological Survey, allowed me to borrow the figured paratype of *Waitara liratula* Powell.

Thanks are also due to Dr. G. Archey, Director of the Auckland Institute and Museum, for permission to reproduce Powell's text-figures of the protoconchs of *Waitara liratula* and *Cryptodaphne pseudodrillia* ; to Drs. T. Kuroda and T. Habe, of Kyoto University, for permission to reproduce their text-figure of the protoconch of *Thatcheria mirabilis* ; to Mr. D. L. F. Sealy, who copied those text-figures and made the original drawings of the protoconchs of *Clinura calliope* and *C. trochlearis* ; and to Mr. N. P. G. Tanti, who took some of the photographs.

IX. REFERENCES

ANGAS, G. F. 1877. Descriptions of a new genus of gasteropodous Mollusca from Japan, and of a new species of *Bullia* from Kurrachi. *Proc. zool. Soc. Lond.*, **1877** : 529–530, pl. 54.

BEETS, C. 1943*a*. Beiträge zur Kenntnis der angeblich Oberoligocänen Mollusken-Fauna der Insel Buton, Niederländisch-Ostindien. *Leid. geol. Meded.*, **13** : 256–328, pls. 27–30.

—— 1943*b*. Notizen über *Thatcheria* Angas, *Clinura* Bellardi und *Clinuropsis* Vincent. *Leid. geol. Meded.*, **13** : 356–367, pls. 36, 37.

—— 1951. On some genera of the family Turridae described from New Zealand. *Basteria*, Lisse, **15** : 14–25, pls. 1, 2.

—— 1953. Reconsideration of the so-called Oligocene fauna in the asphaltic deposits of Buton (Malay Archipelago). *Leid. geol. Meded.*, **17** : 237–258, pl. 1.

BELLARDI, L. 1841. Descriptions des Cancellaires fossiles des terrains tertiaires du Piémont. *Mem. R. Accad. Torino* (2) **3** : 1–42, pls. 1–4. (Paginated 225–264 in whole volume.)

—— 1847. Monografia delle Pleurotome fossili del Piemonte. *Mem. R. Accad. Torino* (2) **9** : 1–122, pls. 1–4. (Whole volume published in 1848, with this article paginated 531–650.)

—— 1875. Novae Pleurotomidarum Pedemontii et Liguriae fossilium, dispositionis prodromus. *Boll. Soc. malacol. ital.*, Pisa, **1** : 16–24.

—— 1877. I molluschi dei terreni terziari del Piemonte e della Liguria, II. Gasteropoda (Pleurotomidae). *Mem. R. Accad. Torino* (2) **29** : 1–364, pls. 1–9. (Whole volume published in 1878.)

BROCCHI, G. B. 1814. *Conchiologia fossile subapennina con osservazioni geologiche sugli Apennini e sul suolo adiacente*, **2** : 241–712, 16 pls. Milano.

—— 1843. 2nd edition of the same work : 1–556, 16 pls. Milano.

COSSMANN, M. 1889. Catalogue illustré des coquilles fossiles de l'Éocène des environs de Paris, faisant suite aux travaux paléontologiques de G.-P. Deshayes. 4ème fascicule. *Ann. Soc. malac. Belg.*, Bruxelles, **24** : 3–381, pls. 1–12.

—— 1896. *Essais de paléoconchologie comparée*, **2** : 1–179, 8 pls. Paris.

—— 1901. *Essais de paléoconchologie comparée*, **4** : 1–293, 10 pls. Paris.

COX, L. R. 1955. Observations on gastropod descriptive terminology. *Proc. malac. Soc. Lond.*, **31** : 190–202, figs. 1–9.

DALL, W. H. 1908. The Mollusca and the Brachiopoda. *Bull. Mus. comp. Zool. Harv.*, Cambridge, Mass., **43** : 205–487, pls. 1–22.

EALES, N. B. 1938. On the affinities of *Thatcheria mirabilis* Angas. *Proc. malac. Soc. Lond.*, **23** : 15–17, figs. 1, 2.

EAMES, F. E. 1957. Eocene Mollusca from Nigeria : a revision. *Bull. Brit. Mus.* (*nat. Hist.*), London (geol.) **3** : 23–70, pls. 5–10.

FISCHER, P. 1880–1887. *Manuel de conchyliologie et de paléontologie conchyliologique.* xxii + 1369 pp., 24 pls. Paris.

FORESTI, L. 1868. Catalogo dei molluschi fossili Pliocenici delle Colline Bolognesi. *Mem. R. Accad. Bologna* (2) **7** : 541–638, pls. 1, 2.

FRIEDBERG, W. 1912. Mięczaki mioceńskie ziem polskich (Mollusca miocenica Poloniae), II. *Wydaw. Muz. Dzieduszyck.*, Lwów, **14** : 113–240, pls. 6–14.

GLIBERT, M. 1960. Les Conacea fossiles du Cénozoïque étranger des collections de l'Institut Royal des Sciences Naturelles de Belgique. *Mém. Inst. Sci. nat. Belg.*, Bruxelles (2) **64** : 1–132.

GRANT, U. S. & GALE, H. R. 1931. Catalogue of the marine Pliocene and Pleistocene Mollusca of California and adjacent regions. *Mem. S. Diego Soc. nat. Hist.*, **1** : 1–1036, pls. 1–32.

HABE, T. 1955. *Thatcheria mirabilis* Angas (Turridae). *Illustrated catalogue of Japanese shells* (B), Nos. 16a, 16b : 2 pp., 3 figs.

HATAI, K. & NISIYAMA, S. 1952. Check list of Japanese Tertiary marine Mollusca. *Sci. Rep. Tôhoku Univ.*, Sendai (2) special vol. **3** : 1–464.

HIRASE, S. 1934. *A collection of Japanese shells with illustrations in natural colours.* xvi + 217 pp., 130 pls. Tokyo.

HIRASE, S. & TAKI, I. 1954. *An illustrated handbook of shells in natural colors from the Japanese Islands and adjacent territory* (2nd edition). xxiv + 124 pp., 134 pls. Tokyo.

HOPWOOD, A. T. 1937. Report of Ordinary Meeting of the Malacological Society of London held on Friday 8th January 1937. *Proc. malac. Soc. Lond.*, **22** : 158–159.

HÖRNES, M. 1851–1856. Die fossilen Mollusken des Tertiaer-Beckens von Wien. *Abh. geol. Reichsanst., Wien,* **3** : 1–736, atlas 52 pls.

HÖRNES, R. & AUINGER, M. 1891. *Die Gasteropoden der Meeres-Ablagerungen der ersten und zweiten miocänen Mediterran-Stufe in der österreichisch-ungarischen Monarchie,* **8** : 331–382, pls. 43–50. Wien.

KIRA, T. 1955. *Coloured illustrations of the shells of Japan.* 8 + 204 pp., 67 pls. Osaka.

KURODA, T. & HABE, T. 1952. *Check list and bibliography of the Recent marine Mollusca of Japan.* 210 pp., 2 maps. Tokyo.

KURODA, T. & HABE, T. 1954. Notes on three remarkable species of Japanese gastropods. *Venus, Kyoto,* **18** : 79–84, figs. 1–4.

MACNEIL, F. S. 1960. Tertiary and Quaternary Gastropoda of Okinawa. *Prof. Pap. U.S. geol. Surv.*, Washington, **339** : i–iv, 1–148, 21 pls.

MARTIN, K. 1933. Eine neue tertiäre Molluskenfauna aus dem Indischen Archipel. *Leid. geol. Meded.*, **6** : 7–32, pls. 1–5.

MARWICK, J. 1926. New Tertiary Mollusca from North Taranaki. *Trans. N.Z. Inst.*, Wellington, **56** : 317–331, pls. 73–75.

—— 1931. The Tertiary Mollusca of the Gisborne district. *Palaeont. Bull. N.Z.*, Wellington, **13** : 1–177, pls. 1–18.

MAYER-EYMAR, C. 1896. Descriptions de coquilles fossiles des terrains tertiaires inférieurs (suite). *J. Conchyliol.*, Paris, **43** (**1895**) : 40–54, pls. 2–4.

MILLET, P.-A. 1826. Sur un nouveau genre de coquilles de la famille des Zoophages. *Mém. Soc. linn. Paris,* **5** (**1827**) : 437–441, pl. 9.

OTUKA, Y. 1949. Fossil Mollusca and rocks of the Kiyosumi Group exposed at Minato-machi, Chiba Prefecture, and its environs (1st paper). *Jap. J. Geol. Geogr.*, Tokyo, **21** : 295–313, pl. 13.

PCHELINTSEV, V. F. & KOROBKOV, I. A. 1960. Gastropods. *Osnovy paleontologii.* 360 pp., 28 pls. Moskva.

PILSBRY, H. A. 1895. *Catalogue of the marine mollusks of Japan, with descriptions of new species and notes on others collected by Frederick Stearns.* i–viii, 1–196, 11 pls. Detroit.

POWELL, A. W. B. 1942. The New Zealand Recent and fossil Mollusca of the family Turridae, with general notes on Turrid nomenclature and systematics. *Bull. Auckland Inst.*, **2** : 1–188, pls. 1–14.

ROSSI RONCHETTI, C. 1951–1956. I tipi della " Conchiologia fossile subapennina " di G. Brocchi. Supplement to *Riv. ital. Paleont.*, Parma, **57–62** : 1–343 and indices, figs. 1–185.

SACCO, F. 1889. Louis Bellardi : notice biographique et bibliographique. *Ann. Soc. malac. Belg.*, Bruxelles, **24** : v–vij.

SCHILDER, F. A. 1932. Cypraeacea. *In* Quenstedt, W., *Fossilium Catalogus,* **55** : 276 pp. Berlin.

SOWERBY, G. B. 1870–1880. *Thesaurus conchyliorum, or Monographs of genera of shells,* **4** : 260 pp., 137 pls. London.

STEWART, R. B. 1927. Gabb's California fossil type gastropods. *Proc. Acad. nat. Sci. Philad.*, **78** (**1926**) : 287–447, pls. 20–32.

THIELE, J. 1929–1931. Loricata, Gastropoda. *Handbuch der systematischen Weichtierkunde,* **1** : i–vi, 1–778, figs. 1–783. Jena.

—— 1934–1935. Scaphopoda, Bivalvia, Cephalopoda [mit Nachträgen und Berichtigungen zum 1. Band] ; vergleichende Morphologie, usw. *Handbuch der systematischen Weichtierkunde,* **2** : i–v, 779–1154, figs. 784–897. Jena.

TOMLIN, J. R. LE B. 1919. Editorial notes. *J. Conch.*, London & Leeds, **16** : 66–67.

TRYON, G. W. 1881. Tritonidae, Fusidae, Buccinidae. *Manual of Conchology, structural and systematic,* **3** : 1–310, pls. 1–87. Philadelphia.

TRYON, G. W. 1883. *Structural and systematic conchology : an introduction to the study of the Mollusca.* **2** : 1–430, pls. 23–91. Philadelphia.

VINCENT, E. 1913. Contribution à la paléontologie des falaises de Landana (Bas-Congo) : Mollusques. *In* Vincent, E., Dollo, L. & Leriche, M., La faune paléocène de Landana. *Ann. Mus. Congo belge 4to,* Bruxelles, A (3) **1** : 1–92, pls. 1–10.

WENZ, W. 1938–1944. Gastropoda : allgemeiner Teil und Prosobranchia. *In* Schindewolf, O. H., *Handbuch der Paläozoologie,* **6** : xii + 1639 pp., 4211 figs. Berlin.

WOLF, H. 1870. Die Stadt Oedenburg und ihre Umgebung. *Jb. geol. Reichsanst., Wien,* **20** : 15–64, pl. 3.

WRIGLEY, A. 1939. English Eocene *Surculites. Proc. malac. Soc. Lond.,* **23** : 277–284, pl. 18.

YOKOYAMA, M. 1928. Pliocene shells from Hyuga. *J. Fac. Sci. Tokyo Univ.* (2) **2** : 331–350, pls. 66, 67.

—— 1930. On a univalve called *Cochlioconus gradatus* Yokoyama. *J. Fac. Sci. Tokyo Univ.* (2) **2** : 405–406, 1 fig.

BRITISH MUSEUM 17 JUL 1963 NATURAL HISTORY

PLATE 47

Thatcheria mirabilis Angas

Holotype : British Museum (Nat. Hist.), no. 1960.154.
Recent ; off Japan.

Fig. 1.—Apertural view. ×1.
Fig. 2.—Apical view. ×1.
Fig. 3.—Oblique view of ramp to show growth-lines. ×2.

Thatcheria vitiensis sp. nov.

Holotype : British Museum (Nat. Hist.), no. G. 91124.

Lower Pliocene ? (marls of Vanua Levu Formation) ;
near Savusavu, Eastern Vanua Levu, Fiji.

Fig. 4.—Apertural view. ×1½.
Fig. 5.—Apical view. ×1.
Fig. 6.—Oblique view of ramp to show growth-lines. ×2.

Thatcheria liratula (Powell)

Paratype : New Zealand Geological Survey, no. TM. 2864.

Lower Pliocene (Opoitian) ; N.Z.G.S. loc. 1543, mudstone and argillaceous sandstone beds, Mangawhero Stream, Taramarama (S.W.) S.D., Wairoa, New Zealand.

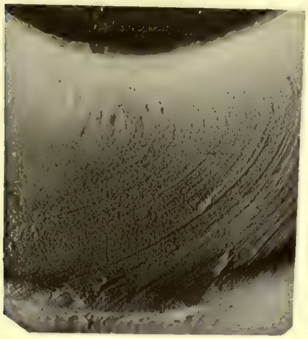
Fig. 7.—Lateral view of spire. ×2½.
Fig. 8.—Oblique view of ramp to show growth-lines. ×6.

Clinura calliope (Brocchi)

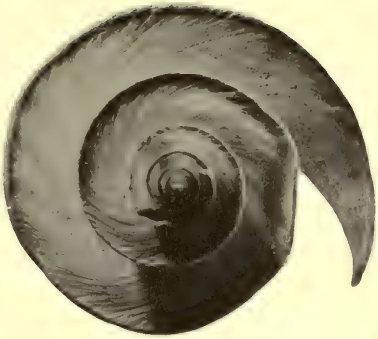
British Museum (Nat. Hist.), no. G. 79439.

Lower Pliocene (Plaisancian) ; Biot, near Antibes,
Alpes Maritimes, France.

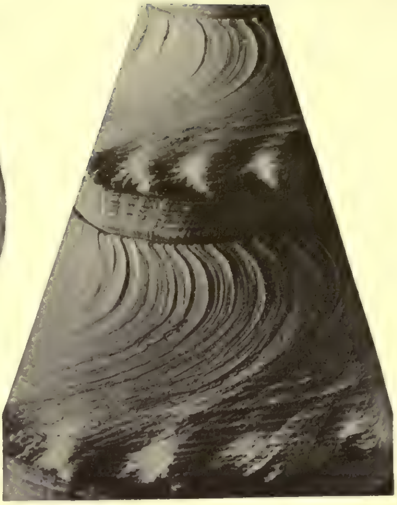
Fig. 9.—Apertural view. × about 1½.
Fig. 10.—Abapertural view. × about 1½.
Fig. 11.—Oblique view of ramp to show growth-lines. ×5.
Fig. 12.—Protoconch and early whorls of teleoconch. × 125.



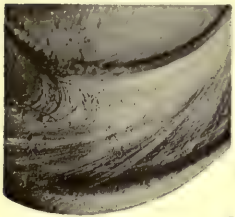
3



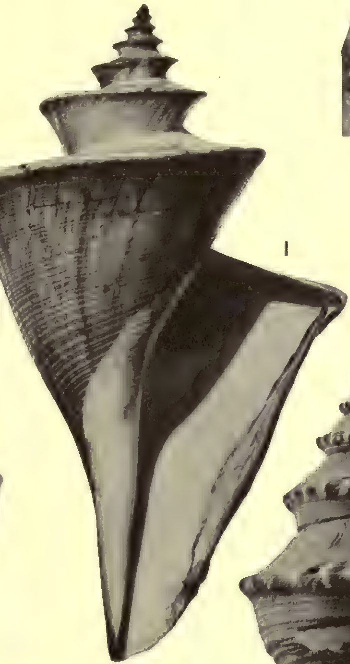
2



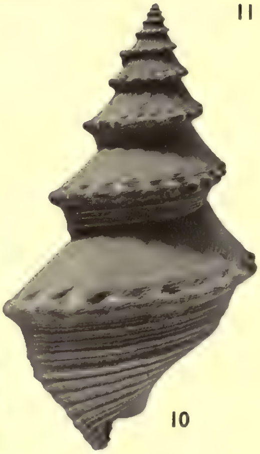
11



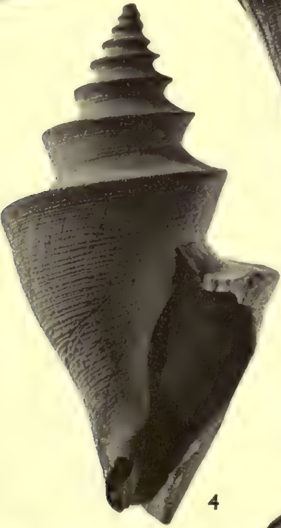
6



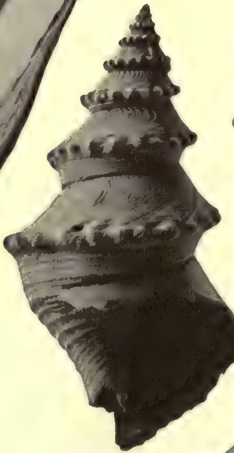
1



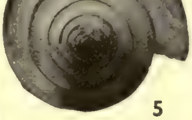
10



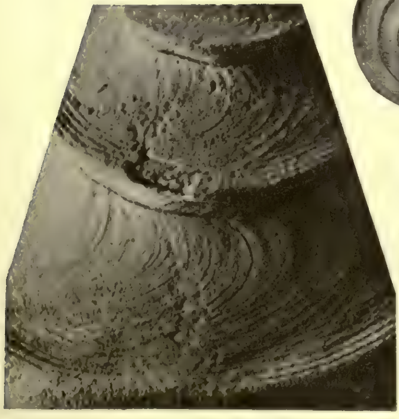
4



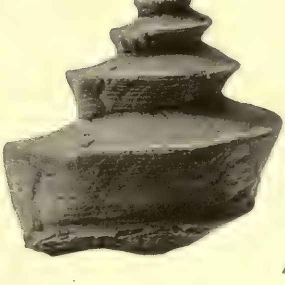
9



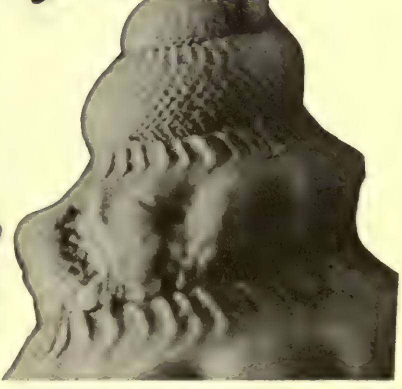
5



8



7



12

BRITISH
17 JUL
NATURAL

INDEX TO VOLUME VII

New taxonomic names and the page numbers of the principal references are printed in **Bold** type.
An asterisk (*) indicates a figure

Abbass, H. L. 173–196
Abbey Wood, Kent 6, 8
Acaste alifrons 100, 103
  exilis 100
Acastinae 97
Acidaspis caractaci 239
  harnagensis 237
  magnospina 123
  primordialis 122, 237
  semievoluta 69, 122
  sp. 123
Actaletes neptuni 156
Adapidae 14, 21, 24, 25, 27, 31, 32, 34
Adapis 4, 10, 12–15, 17–23, 30, 32
  angustidens 33
  magnus 17, 19, 33
  minimus 13
  parisiensis 10, 18, 25, 29, 30, 33
  priscus 33
  rutimeyeri 33
  sciureus 33
Aeluravus 29
Aeschna 163
  liassina 164
Akera 260
Akeridae 267
Alsaticopithecus 25, **31**, 33
  leemanni 25, 27, 31, 33
Alternata limestone 219
Amphilemur 25, 33
  eocaenicus 25, 33
Amphilemuridae 23, 25
Amphitryon 251
  radians 220
Amplexograptus perexcavatus 232
Ampyx linleyensis 78
  pennatus 78
  rostratus 76, 78
  salteri 78
  tetragonus 78
Anachoropteris 208
  involuta 208
Anagale 27
Anaptomorphidae 3, 24, 27
Anchomomys 3, 19, **21**, 23, 31, 33, 34
  gaillardi 33
Anchomomys—contd.
  latidens 21–23, 31, 33
  pygmaeus 33
  quercyi 21, 22*, 33
Anisozygoptera 155, 160
Anthropoidea 17
Anticlinura 263, 266
Anulatisporites anulatus **147** ; Pl. 22, figs. 70, 71
  sp. **148**; Pl. 22, fig. 72
Aotes 5
Apatemyidae 23, 26
Aphanolemur 15
  gibbosus 15
Aphelotherium 32
Apiculatisporites 150
Apotropteris 208
Apterygota 156
Archaeopteridium 142
  tschermaki **142** ; Pl. 21, fig. 22
Archimediella 178
Architemidae 164
Arcotia 179
Asaphidae 229
Asaphinae 229
Asaphus marstoni 231
  powisi 229, 232
  seticornis 85
Asperdaphne versvestita 277
Asplenium 207
Asteroceras obtusum 155, 161
Atractopyge **91**, 93, 130
  aspera 91
  atractopyge 93
  michelli 93
  scabra 91, 92, 93 ; Pl. 11, figs. 2, 3, 10
  sp. **93**, 94, ; Pl. 11, figs. 5, 8
Auckland Institute & Museum 294
Aurelia aurita 156
Azonotriletes 150

Balanus improvisus 156
Bancroftina typa 71
  Zone 80, 93, 107, 125
Basilicus 229
  marstoni 229
  powisi 229, 232

Birbal Sahni Institute 151
Birmingham University 137, 151
Blattodea 158
Bourguetia saemanni 194
  striata 194
Bothrodendron tenerrimum 139
Broeggerolithus 79–82, 129
  broeggeri 79
    Zone 221, 232
  globiceps 71, 84
  longiceps 71, 81–83
  melmerbiensis 81 ; Pl. 6, figs. 10, 13
  nicholsoni **79**, 80–83, 129 ; Pl. 6, figs. 7, 11 ; Pl. 7, figs. 1–12
  simplex 79, 81
  soudleyensis 84
  sp. 79, **83** ; Pl. 8, fig. 2
  transiens 81, **82**, 83, 84, 129, 218 ; Pl. 8, figs. 1, 3, 4, 6, 8, 11
Brongniartella 82, **106**, 129
  ascripta **106**, 107, 108, 110 ; Pl. 15, figs. 1, 2, 5, 8, 11 ; Pl. 16, fig. 14
  bisulcata 107, **108**, 109, 110, 129 ; Pl. 16, fig. 8
  depressa 108, 109, 110 ; Pl. 16, figs. 1, 7, 10, 13
  minor **106**, 107 ; Pl. 15, fig. 4, ; Pl. 16, fig. 11
    subcarinata 107, 110
  parva 106
  platynota **110**
  rudis 107
  sp. 108
Buccinidae 259, 267, 289
Burrirhynchia 42, 43, **58**, 59
  cantabrigensis 42, 59*, **60**, 61
  leightonensis **59**, 60, 61

Caenopithecus 14, 19, 21, 27, **29**, 30, 31, 33, 34
  lemuroides 29, 33
Calamospora 144, 150
  mutabilis **144**, Pl. 22, fig. 44
  sp. **144** ; Pl. 22, fig. 44
Calathiops sp. **143** ; Pl. 21, figs. 27–29
Calliops brongniarti 104
  jukesi 100
  var. *vicina* 104
Calymene 111
  aldonensis 113
  bigener 113
  blumenbachii var. *caractaci* 114, 216, 217, 225
  brevicapitata 223
  callicephala 111
  caractaci 111, 217
  diademata 116
  fatua 219
  forcipata 235, 236
  grayae 113
  incerta 219
  meeki 111
  odini 104
  planimarginata
Calymene—contd.
  pulchra 220
  quadrata 113, 227
  senaria 111
  verrucosa 91
Calymenidae **111**, 215, 216
Calyptaulax **98**, 130
  actonensis 100
  altumi 99, 100
  compressa 100
  glabella 98, 100
  norvegicus 98, 99
  planiformis 98, 99, 100 ; Pl. 13, figs. 1–5
  schucherti 100
  sp. 98, 99
Camptotriletes sp. **146** ; Pl. 22, fig. 58
Cantius 3, 4, **5**, 6, 8, 10, 14, 22, 34
  eppsi 4, 6, 7, **8**, 9, 32 ; Pl. 1
Capillae 42
Capillirhynchia wrighti 44
Cardium edule 156
Carpolestidae 24
Ceciliolemur 27, **30**
Ceratopogon 156
Ceraurus octolobatus 88
Cerithiacea 180
Cerithium turritellatum 183
  unicarinatum 182
CHARIG, A. J. 255–297
Charmouth, Dorset 155
Chasmops **104**, 129, 248
  conicophthalma 106
  extensa **104**, 106, 115, 229 ; Pl. 13, fig. 8
  jukesi 100
  maxima **105** ; Pl. 13, fig. 6
  sp. **105** ; Pl. 13, fig. 12
Chasmopsinae 104
Cheiruridae 86
Cheirurus octolobatus 88
Chironomus 156, 157
Chomatopyge 119
Chondrites plumosus 150
Chondrosteus sp. 155
Chonetoidea 115
  sp. 84
Cibotium barometz 205
  regale 205, 206
Cirratriradites 150
  sp. **148** ; Pl. 23, fig. 74
Clavatulinae 262
Clinura 257, 262–264, 266, 268, 270, 271, 272*, 273, 277–283, 286–289, **291**
  bituminata 262, 279–282, 286, 291
  calliope 263, 266, 271–274, 275*, 276, 278–280 282, 286–288, 290, 294
  carinata 279–282
  controversa 279, 280, 287, 288, 291
  elegantissima 263, 279
  generosa 286, 288, 291
  monochorda 263

Clinura—contd.
  peruviana 263
  sabatiorum 279, 291
  sopronensis 279, 291
  subtrochlearis 291, 279
  Thatcheria group 278, 286, 288
  trochlearis 271, 272, 274, 275*, 279, 280, 286, 288, 290, 291, 294
  waitaraensis 286, 291
Clinuromella 263
Clinuropsis 262, 263, 266, 278–280
  calliope 266
  monochorda 263
Cochlespirinae 261, 266, 290
Cochlioconus 260–262, 265, 267, 268, 270, 278–280, 288, 292
  gradatus 259, 260, 265
Coenopterideae 210
Coleoptera 159, 167
Colpocoryphe aldonensis 113
Colposigma 179
Conidae 261, 267, 268, 277, 288, 289
Conolichas **120**, 129
  melmerbiensis **120**, 121 ; Pl. 17, figs. 14, 16 ; Pl. 18, figs. 1–4
Conorbiinae 261
Conularia 150
Conus 259–261, 267, 268
  araneosus 288
  pennaceus 277
  quercinus 260
Convolutispora sp. **146** ; Pl. 22, fig. 59
  tessellata 146
Coryphodon 8
Costellae 42
Costonia ultima Zone 235
Craeseops 25
Craiginia 179
Cretaceous Gastropoda 173–196
Cretirhynchia 39, 43, 59–61
  norvicensis 58*, 61
  octoplicata 49
  plicatilis 60
Cristatisporites 150
Croft, W. N. 197–211
Cryptoconus 262, 279, 292
Cryptodaphne pseudodrillia 275*, 294
Cryptolithinae 79
Cryptolithus broeggeri 79
  gracilis 84
  nicholsoni 79
  transiens 82
Cryptothyris paracyclica 71
Cupedidae 167, 169
Cupes 167
  capitatus 167
Cybele loveni 94
  var. *girvanensis* 94
  verrucosa 91, 93
Cybelinae 91
Cyclogranisporites 150
  amplus **145** ; Pl. 22, figs. 49–51
  orbicularis 145
  sp. **145** ; Pl. 22. fig. 52
Cyclostigma 138
Cyclothyrid **42**
Cyclothyrinae 39, 43
Cyclothyris **39***, 40*, 41*, 42, **43**
  americana 40
  antidichotoma 41, 42, 44, **47**, 48*, 49*, 56 ; Pl. 4, figs. 3–6
  compressa **54**, 61 ; Pl. 5, fig. 8
  depressa 41, **50**, 56 ; Pl. 4, fig. 11
  difformis 41, 42, 44, 45, **51**, 52*, 53*, 54, 58 ; Pl. 5, figs. 1–7
  latissima 39, 41, **45**, 46*, 50, 56–58, 60 ; Pl. 4, figs. 7, 8
  lepida 41, 42, **55**, 56, 57 ; Pl. 4, fig. 10
  levis 41, 42, **56**, 57 ; Pl. 4, fig. 9
  plicatilis 60
  scaldisensis 42, 44, 46, **57** ; Pl. 4, fig. 1
  schloenbachi 42, 50, **55**, 56 ; Pl. 4, figs. 12, 13
  subtrigonalis 40
Cynodontomys 25
Cyphaspis jamesoni 126
  megalops 123
  nicholsoni 118
Cypraeacea 266
Cyrtometopinae **86**

Dalmanella horderleyensis 71
    Zone 217, 223
  indica 71
    Zone 222
  lepta 71, Zone 222
  unguis 71, Zone 218, 219, 246
  wattsi 71, Zone 218
Dalmania socialis 95
Dalmanitidae 95
Dalmanitina 95
  mucronata 95, 96
    matutina **95**, 96 ; Pl. 12, figs. 1, 5, 6, 9, 12
Dalmanitinae 95
Dapedium granulatum 155
  sp. 155
Daphnella 277
  cancellata 277
Daphnellinae 257, 261, 265, 267, 277, 289–291
Daubentonia 26
Dean, W. T. 65–134, 213–254
Decoroproetus 126
  fearnsidesi 243
Defrancia pagoda 266
Densosporites 150
  sp. **148** ; Pl. 23, fig. 73
Diacalymene **113**, 114, **116**
  bigener 113
  diademata 113, 114
  marginata **116**, 227 ; Pl. 13, fig. 13 ; Pl. 14, fig. 11

Diacalymene—*contd.*
  praecox 113, 225, 227
Diastatomma liassina 164
Diastatommites 164
  liassina 161, **164** ; Pl. 27, fig. 3
Dicranograptus clingani Zone 72, 226, 232, 242
Dictyotriletes sp. 147 ; Pl. 22, fig. 64
Didymograptus superstes Shales 113
Dimeropyge 119
Dimeropygidae 118, 119
Dindymene 89
  duftonensis 89, 90 ; Pl. 11, fig. 13
  fridericiaugusti 89
  ornata 90
  plasi 90
  sp. 89, **90** ; Pl. 11, fig. 6
Dindymeninae 89
Diplograptus multidens Zone 129, 226, 232
  perexcavatus 232
Diplopteridium 140–143
  holdeni 137, **140**, 142 ; Pl. 20, figs. 8–15
  teilianum 141, 143
Diptera 156, 158
Dolerorthis sp. 77
Drybrook Sandstone 137, 149
Duftonia 69, **97**, 103
  lacunosa **97**

Elcanidae 158, 159
Encrinuridae 88
Encrinurinae 88
Encrinurus **88**, 89
  sp. **88** ; Pl. 11, figs. 1, 4
Endosporites sp. **148** ; Pl. 23, fig. 75
Ensifera 165
Entomolestes 25
Entomostracites crassicauda 233
  laticauda 251
  punctatus 88
Eobronteus 251
  sp. **251** ; Pl. 46, fig. 10
Erinaceoidea 25
Estoniops **100**, 103
  alifrons **100**, 101–104, 129 ; Pl. 12, figs. 2, 4, 7, 8, 10, 13
  exilis 103
  jukesi 101
Europolemur 12, 13, 27, **31**, 33
  klatti 9, 12, 13, 33

Ficidae 259, 267
Ficus 259, 267
Fiji Geological Survey 294
Filicales 201
Flexicalymene 82, 111, **112**, **113**, **114**, 118, 216, 219, 236
  acantha 112, **216**, 217, 219, 220, 225 ; Pl. 37, figs. 1, 3–6, 14
  brevicapitata 112, 220
  cambrensis 112, 219
Flexicalymene—*contd.*
  caractaci 112, **114**, **217**, 218–220 ; Pl. 13, fig. 10 ; Pl. 38, figs. 2, 4–6, 8, 11, 12
  cobboldi 218, 220 ; Pl. 38, figs. 1, 3
  croneisi 223
  declinata 112, 220
  forcipata 112
  horderleyensis 221, 223 ; Pl. 37, figs. 2, 8 ; Pl. 40, figs. 7, 8
  incerta 220
  laticeps 115, 224
  limba 113, **221**, 223 ; Pl. 37, fig. 16
  onniensis 69, 112, **115**, 223 ; Pl. 13, fig. 7 ; Pl. 14, figs. 1, 2, 7, 10
  planimarginata 112, 114, **217**, 219, 220 ; Pl. 37, fig. 15
  pusulosa 113, 217, **220**, 221, 223 ; Pl. 37, figs. 9, 11, 12
  salteri 224
  senaria 112
  shirleyi 112
  sp. 221, 223
  trigonoceps 217, 218
Fucus sp. 156
Furcirhynchia furcata 44
Fusidae 267
Fusinae 267
Fusinidae 267, 289
Fusininae 267
Fusinus 259, 267
Fusus 259, 267

Galago 17, 23
  crassicaudatus 6
Galeodidae 261, 267, 268
Galigidae 23
Gastropoda 175, 180
Geological Society, London 69
Geological Survey & Museum 59, 102, 103, 187, 224, 225, 240, 245
Gesneropithex **31**, 33
  peyeri 27, 31, 33
Glasgow University 137
Glyptocrinus Flags 221
Grammatopteris 208
  baldaufi 209, 201
  rigolloti 209
Granulatisporites 150
  orbiculus **145** ; Pl. 22, figs. 47, 48
  sp. **145** ; Pl. 22, figs. 47, 48
  tenuis 144 ; Pl. 22, figs. 45, 46
Gravicalymene 112, **113**, 114, **117**, 225
  convolva 116, 118, 225, 225
  inflata 227 ; Pl. 39, fig. 6
  jugifera 116, 118, 226 ; Pl. 13, figs. 9, 11 ; Pl. 14, figs. 3, 4, 8, 9
  praecox 112, 216, **225**, 226–228 ; Pl. 39, figs. 1, 3, 9, 12–14
  sp. 227
Gryllacrididae 155,166

Hagla 165, 166
Haglinae 165
Halle University 12, 34
Harknessella subquadrata Zone 220, 235, 245
Harpalideous Carabidae 168, 170
Harpalus schlotheimi 168
Haustator 178, 184, 187, 191
  granulata 183, 184
  granulatoides 183, 184
Hemiacodon 4–8
Hemifusus 259, 261, 267, 268
Heterophlebia westwoodi 161
Heterorthis alternata 219
Hirnantia sagittifera 71
Hoanghonius 4
Holcoëlytrum 155, 167
  giebeli 167, **168**, 170, 171 ; Pl. 27, figs. 6–8
  schlotheimi 168, **170**, 171 ; Pl. 27, fig. 5
Holcoptera 168
Holden, H. S. 197–211
Homalonotidae 106
Homalonotus ascriptus 69
  bisculatus 106, 108
    var. *minor* 106
  rudis 107
Homalops altumi 99, 100
Homolichas melmerbiensis 120
Homolochinae 120, 235
Hydrobia 157
Hydrophilidae 157
Hymenoptera 159
Hyracotherium 8

Illaenidae 120, 233
Illaenus 129, 233
  bowmani 120
  fallax **233**, 234
  linnarssoni 120
  sp. 233
Imperial College of Science, London 175
Inoceramus 155
Insectivora 25
Ireland National Museum 235, 236
Isotelinea 229
Isotelus brachycephalus 233
Isotelus powisi 229

Jurassobatea gryllacroides 166

King's College, London 61
Kingston Technical College 137, 151
Kjaerina bipartita Zone 71, 89, 219
  geniculata 77, 91
  typa Zone 71, 91, 218
Kjerulfina polycyma 83
Kloucekia **97**
  apiculata 72, **97**, 129 ; Pl. 12, fig. 11
Knoxisporites 147
Kyoto University 294

Lacunosella 43
Lamellaerhynchia 43, 60
  larwoodi 41
Leiotriletes sphaerotriangularis **143** ; Pl. 21, figs. 30, 31
Lele, K. M. 135–152
Lemuridae 24
Lemuriformes 5
Lemuroid Primates, Concept of **23**
Lepidophyllum fimbriatum 137, 138, **139**, 140, 150 ; Pl. 20, figs. 18–20
Lepidorhynchia 43, 60
Lepidosigillaria whitei 140
Lepidostrobophyllum fimbriatum 138
Leptadapis 32
Leptocolpus 179
Leucosyrinx circinata minatoensis 290
Leymeriella tardefurcata Zone 41, 42, 50, 56, 57, 59, 60
Liassocupes 167
  parvus 167 ; Pl. 27, fig. 4
Liassophlebia **161**
  gigantea 163 ; Pl. 27, fig. 2
  jacksoni 162, 163, 164, ; Pl. 25
  magnifica 161, **162**, 163, 164 ; Pl. 27, fig. 1
  sp. **164**
  withersi 164
Liassophlebiidae **160**
Lichas aculeatus 235
  aequiloba 120
  laxata 121, 235
  margaritifer 121, 235
  melmerbiensis 69, 120
  nodulosus 121, 235
  segmentatus 235
  sexspinus 235
  verrucosa 234
Lichidae 120, 234
Lichinae 234
Lipura maritima 156
Lonchodomus 72, 77, 78
  carinatus 78, 79
  pennatus 77, **78**, 79, 84, 129 ; Pl. 6, figs. 1, 3–5, 9, 12
  politus 77
  rostratus 72, 77
  swindalensis 72, 77 ; Pl. 6, figs. 2, 6, 8
London Clay 3
Lophotriletes 150
Loris 18
  tardigradus 18
Lushius 4
Lycospora 150
  bracteola **147** ; Pl. 22, fig. 65
  granulata 147
  spp. **147** ; Pl. 22, figs. 66–69

Macrocranion 25
Manchester Museum 140, 150

Mangeliinae 289
Mathilda 179, 191
  ahmadi 175, 177, 178, 181*, **193** ; Pl. 32, fig. 24
  coxi 175, 177–179, 181*, **191**, 192, 193 ; Pl. 32, fig. 23
  douvillei 192
  faucignyana 192
  quadricarinata 192
Mathildidae 175, 191
Matonia pectinata 205
Mayeria 259, 267
Mecoptera 158
Megachiromyoides 27, **29**
Megasurcula 289
  keepi 289
Megatarsius 13, 14, 27, **31**, 33
  abeli 9, 12, 13, 33
Melongenidae 259, 267
Melongeninae 259, 267
Menocephalus nicholsoni 119
Mesalia 178
Mesotaphraspis 119
Metacupes harrisi 167
  huebneri 234
Metopolichas 234
  patriarchus 234
  sp. **234** ; Pl. 43, figs. 3, 4, 6, 7
  verrucosa 234
Microchoerus 4, 31
  edwardsi 31
  erinaceus 31
  ornatus 31
Microreticulatisporites 150
  cribellarius **146** ; Pl. 22, figs. 60, 61
  spp. **146** ; Pl. 22, figs. 62, 63
Microsyopidae 23, 25, 33
Microsyops 25
Microtarsioides 27, **30**
Murex 263, 271
  calliope 266, 272, 291

Nannopithex 19, 24, 32
  filholi 32
  pollicaris 32
  raabi 32
Navajovius 7, 24
Necrolemur 4, 5, 15, 17, 22, 31, 32
  antiquus 32
  edwardsi 31
  filholi 32
  parvulus 32
  raabi 32
  zitteli 32
Necrolemurinae 4, 23, 31
Nekewis 262, 279
  io 273
Nemagraptus gracilis Zone 77, 113, 129, 226, 232
Nereis diversicolor 156
Nerinaea unicarinata 182
Neuroptera 158
New Zealand Geological Survey 294
Notharctidae 5, 17, 24, 34
Notharctus 6, 12, 14, 15, 17, 30
Notopamphagopsis bolivari 166
Nycticebus 5, 15, 18–20
  cougang 18, 20

Odonata 156, 158, **160**
Odontopleuridae 122, 237
Odontopleurinae 237
Ogmocnemis 126, 243
  calvus 126, 243, 245
Olenidae 241
Omomyidae 3–5, 7, 24, 32, 34
Omomyinae 3
Omomys 4, 6, 7, 30, 32
  belgicus 32
Onnia **84**, 130
  cobboldi Zone 71, 224, 234, 237
  gracilis **84**, 129 ; Pl. 8, figs. 12, 13
    Zone 71, 78, 85, 92, 95, 99, 115, 122, 128, 223, 224, 226, 228, 234
  ornata 220
  superba 129
    pusgillensis **84**, 130 ; Pl. 8, figs. 5, 7, 9, 10
    Zone 71, 78, 84, 85, 88, 92, 95, 99, 115, 128, 224, 242, 251
Onnicalymene 104, **112**, 113, **115**, 129, 223
  jemtlandica 113
  laticeps 113, **115**, **224** ; Pl. 14, figs. 5, 6; Pl. 38 figs. 7, 10, 14, 15
  salteri 113, **224** ; Pl. 38, figs. 9, 13
  onniensis 84, 113, **115**, 129, **223**, 224 ; Pl. 39, figs. 2, 10, 11 ; Pl. 40, fig. 9
Onniella 104, 115, 248
  broeggeri 71, 84
  inconstans 71
  reuschi Zone 71, 83, 218, 240
Orbirhynchia 45
Ordovician trilobites 215
Orimops 111
Orthophlebia 158
Orthophlebiidae 158
Orthoptera Saltatoria 158, **165**
Osmundaceae 210
Otarion **123**, 242
  diffractum 123, 242
  isoplates 124
  planifrons 123, 124
  sp. **123**, **242** ; Pl. 17, figs. 4, 12 ; Pl. 45, fig. 1
Otarionidae 123, 242
Ourayia 6, 18
OWEN, E. F. 37–63

Palaeolemur 32
Parabasilicus 229
  marstoni 231, 232
  powisi **229**, 230–233 ; Pl. 40, figs. 1, 3–5 ; Pl. 41, figs. 1, 2 ; Pl. 42, fig. 9

Parabasilicus—contd.
  shirakii 232
  typicalis 229
Paracybeloides **94**, 129
  girvanensis **94**, 95, 96 ; Pl. 11, figs. 7, 9, 12, 14, 15
  sp. **95**, 103 ; Pl. 11, fig. 11
Parahoplites nutfieldensis Zone 42, 46, 50
Pareora 189
Paromomyidae 24, 27
Pelycodus 6, 7, 14, 18, 29, 30, 32
  helveticus 32
Periconodon 4, **30**, 32
  helveticus 30, 32
Perodicticus 12
Petrophlebia 160, 161
  anglicana 160, 161
  anglicanopsis 159, **160**, 161 ; Pl. 24, figs. 1, 2
Phacopidina **97**
  apiculata **97** ; Pl. 12, fig. 11
  harnagensis 97
Phacops alifrons 100,103
  apiculatus 97
  brongniarti 98
  jukesi 100–103
    var. *vicina* 104
  panderi 103
  phillipsi 97
Phaneropterinae 166
Pharostoma pulchrum 220
Phenacolemur 26, 27
Phenacolemuridae 24
Pholidophorus sp. 155
Planisporites 150
  delucidus 145
  granifer **146** ; Pl. 22, fig. 56
  minimus **145** ; Pl. 22, figs. 53–55
  sp. **146** ; Pl. 22, fig. 56
Platycalymene 111
Platylichas **121**, 122, 235
  laxatus 71, **121**, 122, **235**, 236, 237 ; Pl. 43, figs. 1, 2, 5, 8–12
  melmerbiensis 120, 121
  sp. 122
Plesiadapidae 24, 27
Plesiadapis 26, 27, 33
Pleurofusia 289
Pleurograptus linearis Zone 72, 100, 226
Pleurotoma 262, 263, 271, 274, 279, 288, 291
  calliope 273, 288
  controversa 288
Pleurotomella 263
  calliope 266, 274
  monochorda 263
  packardii 266
Pleurotomidae 263, 268, 288
Pleurotomoides 266
Plicarostrum 43
Portlockia apiculata 97
Powell, A. W. B. 294
Primaspis **122**, 237
  ascitus 241
  caractaci 122, 238, **239**, 240, 241 ; Pl. 44, figs. 3, 7, 9, 11, 13, 14
  harnagensis 122, **237**, 238, 241 ; Pl. 44, figs. 1, 4, 6, 8
  semievoluta **122**, 123, 241 ; Pl. 17, figs. 3, 10, 11, 13, 15
Princeton University 34
Proetidae 124, 243
Proetidella **124**, 126, 129, 243, 245
  fearnsidesi 124, 126, **243**, 245, 246 ; Pl. 45, figs. 3–8, 12, 14
  marri 124, 126 ; Pl. 16, figs. 4, 6, 9 ; Pl. 17, figs. 5, 6, 8, 9
  sp. **246** ; Pl. 45, fig. 13
Proetidellinae **124**, 243
Proetus 231
  asellus 245
  decorus 126
  girvanensis 126
  ovatus 245
  sp. 246
Progalago 19, 21–23, 34
  dorae 21
  sp. 22*
Progonophlebia 162
Promicroceras planicosta 155
Pronycticebus 3, 4, 12–15, 17–23, 33, 34
  gaudryi **14**, 16*, 17, 33
Prophalangopsidae 155, 158, 165, 166
Prophalangopsis 166
Prosimii 27, **31**
Prosobranchia 180
Protoadapis 3, 6, 7, **8**, 9, **10**, 12, 13, **14**, 15, 19, 21, 29–34
  angustidens 11*, 12, 33
  brachyrhynchus 11, 33
  copei 9
  curvicuspidens **10**, 11*, 12, 13, 33
  eppsi 3, 5, 8, 10, 32
  klatti **12**, 13, 29, 30, 33 ; Pls. 2, 3
  recticuspidens 10, 33
Protohagla 165, 166
  langi 158, **165**, 166 ; Pl. 26
Psalixylon 208
Pseudoloris 32
  abderhaldini 32
  parvulus 32
Pseudomelaniidae 194
Pseudosphaerexochus **86**, 130
  octolobatus **87**, 88 ; Pl. 10, figs. 7, 9–12
Pseudotoma 262, 289
Pseudotominae 263
Pteronemobius 158
Pterygometopidae **98**
Pterygometopinae **98**
Pterygometopus 100
  grayae 113
  jukesi 101–103

Pterygometopus—contd.
  panderi 103
  sclerops 103
  sp. 97
  trigonocephala 103
Pugilina 261, 267
Punctatisporites 150
  debilis 144
  minutus **143**, 144 ; Pl. 21, figs. 32–37
  spp. **144** ; Pl. 21, fig. 43
  subobesus 144 ; Pl. 21, figs 38–42
Pyrula 259, 267
Pyrulidae 259, 267

Raphiophoridae 72
Reacalymene 112, 219, 220
  croneisi 223
  holtedahli 226
  horderleyensis 221, 223 ; Pl. 37, figs. 2, 8 ; Pl. 40, figs. 7, 8
  limba 113, 220, **221** ; Pl. 37, fig. 16
  pusulosa 112, 113, **220**, 221, 223 ; Pl. 37, figs. 9, 11, 12
  sp. 221
Remopleurella 215, **249**, 250, 251
  burmeisteri **250**, 251 ; Pl. 45, fig. 2 ; Pl. 46, figs. 6, 8, 9, 11, 12
Remopleurides 104, 115, **127**, 129, 246
  biaculeatus 127
  burmeisteri 128
  colbii 127, 128, 246, 249
  dalecarlicus 246
  latus 248
    var. *granensis* 248
    kullsbergensis 128, 248, 249
    onniensis 247, 248, 249 ; Pl. 46, figs. 4, 5
  radians 220, 251
  spp. **127**, **128**, 246, **248** ; Pl. 18, figs. 5–13 ; Pl. 46, figs. 3, 7
  validus 128, 248
  warburgae 246, 247, 248 ; Pl. 46, figs. 1, 2
  wimani 248
Remopleurididae 127, 246
Remysporites 149, 150
  drybrookensis 148 ; Pl. 23, figs. 76–81
  sp. **149** ; Pl. 23, fig. 82
Reticulatisporites 147, 150
Reuschella sp. 77
Reuscholithus reuschi Zone 217, 226, 231, 238, 245
Rhacopteris geikiei 141
  petiolata 141
Rhodea 141
Rhynchonella 39
  antidichotoma 47
  bertheloti 60
  cantabrigensis 42, 60, 61
  compressa 51
  depressa 50, 55
  difformis 51, 53
  elegans 61
Rhynchonella—contd.
  gibsiana 60
  globata 53
  lata 56
  latissima 45
  leightonensis 42, 59–61
  lineolata var. *mirabilis* 47, 48
  nuciformis 41
  schloenbachi 55
  tripartita 60
  vespertilio 61
Rhynchonellacea 43
Rhynchonellidae 39, **43**
Rhynchota 158
Robergiella 250
  sagittalis 250

Saccoloma elegans 205
Saltatoria 158
  Ensifera 166
Sampo 248
Scutellocladus 138
  variabilis 137, **138**, 139 ; Pl. 19, figs. 1–6
Sechuritella 179
Sedgwick Museum, Cambridge 45, 56, 61, 69, 80, 81, 101, 107, 121–123, 175, 185, 188, 191, 193
Semifusus 259, 260, 265, 267
Sespedectes 25
Shrewsbury Museum 221
Sigmesalia 189
Simons, E. L. 1–36
Smilodectes 15, 17
Smith, E. P. 294
Sowerbyella 115
Spathulopteris 141
Sphaerexochus hemicranium 86
Sphenopteridium 141
Sphenopteris 141
  affinis 143
  bifidum 143
  cuneolata **142** ; Pl. 21, fig. 21
  obfalcata **141** ; Pl. 20, figs. 16, 17
Sporae dispersae **143**
Staurocephalus 71, 123
Stenopareia 120, 234
  camladica 120, 234
  sp. 120
Stigmaria **140** ; Pl. 19, fig. 7
Stolmorhynchia 43
Sulcirhynchia 43, 59–61
Sulcus **42**
Surcula 262, 264, 268, 279, 291
  ingens 266
Surculites 257, 262, 264, 266, 267, 273, 279, 280, 289, 291
  bituminatus 262

Tanganyika 199
Tarsiidae 24, 31
Tarsiiformes 5

- *Tarsius* 5, 17, 19, 23, 29
- *Tarsophlebia* 161
- *Teilhardina* 4, 7, 24, 32
  - *belgica* 4, 32
- *Telangium* 143
  - sp. 142, **143** ; Pl. 21, figs. 23–26
- *Tenebrio molitor* 169
- *Terebratula antidichotoma* 47
  - *compressa* 54
  - *deformis* 51
  - *depressa* 50
  - *difformis* 51
  - *dilatata* 53
  - *dimidiata* 51–53
  - *gallina* 51
  - *lata* 39, 45
  - *latissima* 39, 40, 43, 45
  - *scaldisensis* 57
- *Tetonius* 7, 24, 27
- *Tetralichas melmerbiensis* 120
- *Tettigonia* 166
  - *viridissima* 165
- Tettigoniidae 166
- *Thatcheria* **257**, 258, 259, **283**, **292**
  - *carinata* 283–286, 292, 293
  - *gradata* 258, 268, 276, 280, 281, 292, 294
  - *liratula* 282, 285, 290, 292–294
  - *mirabilis* 257, 258, 260, 264–267, **268**, 269–272 275*, 276, 280, 281, 283, 284, 286, 288–290, 292–294
  - *pagodula* 282–286, 292, 293
  - **vitiensis** 257, 281–283, 285, **292**, 294 ; Pl. 47, figs. 4–6
- Thatcheriidae 261, 265, 267, 268, 277, 290
- Thatcheriinae 257, 267, 290, **291**
- Thysanopeltidae 251
- *Toernquistia* **118**, 119, 129
  - *nicholsoni* 118, 119
  - *reedi* **118**, 119 ; Pl. 16, figs. 2, 3
  - *translata* 119
- *Tomiodendron ostrogianum* 139
- *Torquesia* 179, **182**, 184, 187
  - **faizai** 175, 177, 178, 181*, **188** ; Pl. 30, fig. 15
  - *granulata* 177–179, 181*, 182, **183**, 189–191 ; Pl. 30, figs. 10–14
  - *granulosa* 184
  - **hassani** 175, 177, 178, 181*, 188, **189** ; Pl. 28, fig. 2 ; Pl. 29, fig. 9
  - **tamra** 175, 177, 178, 181*, **185** ; Pl. 28, fig. 1
  - *vibrayeana* 177, 178, 181*, **185**–187 ; Pl. 31, figs. 17–22
  - **wagihi** 175, 177, 178, 181*, **187** ; Pl. 29, fig. 6
- Tretaspidinae **85**
- *Tretaspis* **85**, 130, 248
  - *ceriodes* 85
    - *donsi* **85** ; Pl. 10, figs. 4, 6, 8
  - *convergens* **85** ; Pl. 10, figs. 1, 3, 5
  - *granulata* 220
  - *kiaeri duftonensis* **86** ; Pl. 9, figs. 1, 5, 7
    - *radialis* **86** ; Pl. 9, figs. 2–4
- *Tretaspis—contd*
  - *seticornis* 85
    - var. *anderssoni* 85
- Triarthrinae 241
- *Triarthrus* 241
  - *becki* 241
  - *linnarssoni* **241**, 242 ; Pl. 44, figs. 2, 5, 10, 12
  - sp. 241
- *Trichoptera* 156
- Tridactylidae 158
- Trinucleidae 69, 79, 129
- *Trinucleus bucklandi* 220
  - *gibbifrons* 79
  - *goldfussi* 79
  - *nicholsoni* 69, 79
  - *ornatus* 220
  - *seticornis* 79
- *Trochurus nodulosus* 235
- *Tropaeum subarcticum* 46
- *Tubicaulis* 201
  - **africanus** 199, 200*, **201**, 202*, 204*, 205*, 207–209 ; Pls. 33–36
  - *berthieri* 203, 206, 208
  - *multiscalariformis* 207, 208
  - *scandens* 206–209
  - *solenites* 201, 206–209
  - *stewarti* 207, 208
  - *sutcliffii* 207, 208
- Turbinellidae 259
- *Turbo quadricarinatus* 191
  - *terebra* 180
- *Turricula* 262, 289, 291
  - *javana* 260
  - *waitaraensis* 260, 264
- Turridae 257, 260, 261, 263–267, 277, 278, 288, 290, 291
- *Turritella* 178, **180**
  - **ageri** 175, 177, 178, 181*, **190**, 191 ; Pl. 32, fig. 25
  - *cenomanensis* 191
  - *dibleyi* 177, 178, **180**, 181* ; Pl. 29, figs. 7, 8
  - **faizai** 175, 177, 178, 181*, **188** ; Pl. 30, fig. 15
  - *granulata* 177–179, 181*, 182, **183**, 184, 189–191 ; Pl. 30, figs. 10–14
  - *granulatoides* 183, 184
  - **hassani** 175, 177, 178, 181*, 188, **189** ; Pl. 28, fig. 2 ; Pl. 29, fig. 9
  - *imbricataria* 184
  - *multistriata* 191
  - *rigida* 186
  - **sherborni** 175, 177, 178, 181*, **190**, 191 ; Pl. 30, fig. 16
  - **tamra** 175, 177, 178, 181*, **185** ; Pl. 28, fig. 1
  - *tolenasensis* 187
  - *turbinata* 177, 178, 181*, **193**, 194 ; Pl. 32, figs. 26, 27
  - *unicarinata* 178, 180, 181*, **182** ; Pl. 28, figs. 3–5
  - *vibrayeana* 177, 178, 181*, **185**, 186, 187 ; Pl. 31, figs. 17–22

Turritella—contd.
  wagihi 175, 177, 178, 181*, **187** ; Pl. 29, fig. 6
Turritellidae 175, 179*, 180

Vasidae 259
Verrucosisporites sp. **146** ; Pl. 22, fig. 57

Waitara 257, 258, 260–262, 264, 268, 270, 275, 278–281, 288, 291, 292
  generosa 261, 276, 280–282
  liratula 257, 261, **275***, 276, 280–282, 294
  pagodula 261, 280–282
  waitaraensis 280–282
WALTON, J. 135–152
Washakius 5, 7
Wattsella horderleyensis 121
WENNER-GREN FOUNDATION 34

Xancidae 259
Xipheroceras dudressieri 155
  sp. 155

Yorkshire Geological Society 69
Youngia trispinosa 87

Zaria 178
ZEUNER, F. E. 153–171
Zeuneria sp. 166
Zonales 150

BRITISH MUSEUM
2[illegible] AUG 1964
NATURAL HISTORY

PRINTED IN GREAT BRITAIN BY
ADLARD AND SON, LIMITED,
BARTHOLOMEW PRESS, DORKING